

THE ANT LARVAE OF THE SUBFAMILY PSEUDOMYRMECINAE
(HYMENOPTERA: FORMICIDAE)

By

GEORGE C. WHEELER AND JEANETTE WHEELER

Reprinted from
ANNALS ENTOMOLOGICAL SOCIETY OF AMERICA,
Vol. 49, No. 4, July, 1956

THE ANT LARVAE OF THE SUBFAMILY PSEUDOMYRMECINAE (HYMENOPTERA: FORMICIDAE)¹

GEORGE C. WHEELER AND JEANETTE WHEELER

University of North Dakota

This is one of the smaller subfamilies of ants, comprising only four genera and about 160 species². The largest genus is the Neotropical *Pseudomyrmex* with about 100 species; *Tetraponera* with about 60 species is widely distributed in the Old World tropics; *Pachysima* with two species and *Viticola* with only one are confined to the Ethiopian Region. These ants are notorious for their vicious stinging and famous for their association with plants.

Viticola tessmanni is known only from the cavities of *Vitex staudtii* Guerke, a creeper found in very moist parts of the forest in the Belgian Congo. *Pachysima* lives in the peculiar swollen lateral branches of *Barteria*, in which the ants also keep large coccids. These plants occur in West Central Africa and apparently the ants are limited by the range of their host plants. *Tetraponera* is much more widely distributed in the Old World tropics, where it is a comparatively rare ant and where it utilizes a greater variety

of plant cavities including "dead wood, twigs, stems of lianas, acacia spines, etc." (Wheeler, 1922a, p. 106). The Neotropical *Pseudomyrmex* is the most abundant; its numerous species nest in the hollow stems of a variety of plants, both living and dead. They are best known in connection with the bull-horn acacias, from which about half the recorded collections have been made. They defend their host plants by swarming over an intruder and stinging fiercely—as many tourists have found out to their pained sorrow.

It would seem that so much renown would suffice for four genera, but pseudomyrmecine larvae are quite as famous as their adults. This is truly remarkable in the Formicidae, where the larvae have been generally neglected. Emery in 1899 described and figured *Tetraponera* (called *Sima*) and *Pseudomyrmex* (called *Pseudomyrma*) larvae, placing great stress on the antennal rudiments. He used the presence of these rudiments and the slender shape of the larvae to help define the new subfamily Pseudomyrmecinae (called Pseudomyrminae). He mentioned (but

¹Accepted for publication October 10, 1955.

²Based on the numbers recorded by Emery (1921) in the *Genera Insectorum*.

did not name nor recognize the importance of the most distinctive feature of the subfamily—the trophothylax. Wheeler (1918), in developing the idea of trophallaxis, used as part of his illustrative material the well developed trophorhinium, exudatoria and trophothylax of the *Pseudomyrmecinae* [*Pachysima aethiops* and *latifrons*, *Viticicola* (called *Tetraponera*) *tesmanni* and mentioning *Tetraponera alaborens* and *natalensis*]. By 1920 he knew that antennal rudiments were present in many ant genera and were not distinctive of *Pseudomyrmecinae*, but he still used larval structures as part of his subfamily characterization. Wheeler and Bailey (1920) discussed the food pellets of pseudomyrmecine larvae and gave brief descriptions of mature larval anatomy. They recognized the mature larvae of the four genera as a homogeneous group.

These mature larvae do indeed constitute a homogeneous group in respect to body shape, trophothylax and (except *Pachysima aethiops*) body hairs and size of mouth parts. Within a genus, however, the greater the number of species studied the greater the variation encountered. The species of *Pseudomyrmex* are so diverse that they cover nearly the entire range of differences exhibited by the subfamily, exclusive of *Pachysima aethiops*. The latter is so different in body hairs, shape of head and size of mouth parts that, if it were not for the trophothylax, it could be excluded from the *Pseudomyrmecinae*.

The constellation of characters which is shared by these four genera is found nowhere else. However, the long slender subcylindrical body and the numerous short body hairs are found in other ants inhabiting plant cavities (*Asteca*, *Camponotus*, the *Cataulacini* and *Cephalotini*, *Crematogaster* and *Leptothorax*). As we have pointed out previously³ these may well be adaptations to life in the small-bore chambers of twigs. Another distinctive character is the single-hooked dorsal hair. Double-hooked (or anchor-tipped) hairs are common in the Myrmicinae; but single-hooked hairs are rather rare among ant larvae. We have found them in *Lioponera* (Ceraurini), *Echinopla* (Formicidae), *Asteca* (Dolichoderinae) and *Cataulacus* (Myrmicinae). Even the trophothylax, which is the distinctive character of the larvae of the *Pseudomyrmecinae*, is feebly suggested by the praesaepeum⁴ of the Camponotini. But in *Colobopsis*, where it is best developed, the praesaepeum is still far from being the complete pocket found in the *Pseudomyrmecinae*. Nevertheless, praesaepeum and trophothylax are parallel in structure and function.

³Wheeler, G. C., and J. Wheeler, 1954, Jour. Wash. Acad. Sci. 44: 149.

⁴"The shallow depression on the ventral surface of certain ant abdominal somites." G. C. Wheeler and J. Wheeler, 1953, Ann. Entom. Soc. Amer. 46: 180.

The trophothylax was described by Wheeler⁵ in 1918 (pp. 307-308, see under *Pachysima aethiops* below) but was not named until 1920 (p. 47), when he wrote thus: "the swollen ventral portion of the first abdominal segment, just behind the mouth, forms a pocket in which the worker place a [pellet] of food . . . The pocket, which I call the trophothylax . . ." It is, however, formed from the depressed ventral surface of the thorax and elaboration of the first and second abdominal somites (see Pl. II). The dorsal wall of the trophothylax is formed by the depressed ventral surface of the thorax; the posterior wall (or "bottom" of the pocket) is the ventral surface of abdominal somite I; the antero-ventral portion of the second abdominal somite is produced anteriorly to form the ventral wall of the pocket. The side-walls are formed by the ventrolateral projections of the mesothorax and abdominal somite I; if the pocket is partly full the ventrolateral projections of the mesothorax are also involved; when crammed full the ventrolateral projections of the prothorax are also part of the sidewalls. The trophothylax may be emptied (to judge from preserved *Pseudomyrmex gracilis mexicanus* and *Ps. apache* larvae in our collection) by being everted; that is, the depressed surface may be pushed ventrally until it protrudes beyond the lip of the pocket. The integument lining the pocket has many short rows of spinules directed posteriorly (i.e., toward the bottom of the pocket). The head may be moved enough so that the mouth parts are directed posterodorsally and are in contact with the food in the pocket. In this position the opening of the salivary gland is directed at the food pellet. On the other hand, the mouth parts may be directed posteroventrally when the pocket is everted.

⁵Emery (1899, p. 6) had mentioned a depression on the ventral surface of the mesothorax and first abdominal somite in *Tetraponera* (called *Sima*) but said that it was not present in *Pseudomyrmex pallidus* (called *formica*) (see below under the subfamily). Dutt (1912, p. 249) mentioned a depression in *Tetraponera rufonigra* but did not mention a pocket or food-pellets (see below under the species).

⁶Wheeler and Bailey (1920, pp. 257-258): "The sternal portion of the first abdominal segment is transversely elliptical, swollen, protuberant and furnished with a food-pouch, the trophothylax." But their Figures 3 (p. 256) and 4A (p. 257) show the ventrolateral projections of the first abdominal somite lateral to the pocket and—although the lines are slightly ambiguous—the second abdominal somite may be seen to form the ventral surface of the pocket. Donisthorpe and Morley (1945, Proc. Royal Entom. Soc. London 20: 49) defined the trophothylax as "a special large food-sac, situated just behind the mouths of ants of the genus *Pseudomyrmex*. Wheeler." This is confusing on two counts: the pocket as defined by Wheeler was (1) a larval structure (2) of the subfamily *Pseudomyrmecinae*. Gaul (1951, Ann. Entom. Soc. Amer. 44: 484) stated that the trophothylax was "the pocket-like invagination in the first ventral abdominal segment of the larvae of the *Pseudomyrmecinae*. It is used to store food for the workers." The second sentence certainly runs counter to Wheeler's conclusions.

In our preserved material the just-hatched larvae of *Pseudomyrmex alliodorae* show a slight fold in the region of the trophothylax, but comparable larvae of *Tetraponera aitkeni* show a well developed pocket. These younger larvae, however, never show any food in the trophothylax. Some second (?) instar larvae show food-pellets. This suggests that the very youngest larvae may be fed by regurgitation and not with solid food. (See Wheeler, 1928, below.)

We have no young larvae of *Pachysima* showing the large exudatoria described and figured by Wheeler (1918). Even our mature specimens are badly damaged.

Subfamily *Pseudomyrmecinae*? (Emery)

M. R. Smith emend.

Body straight, slender, subcylindrical; anterior end more rounded than the posterior end; head applied to the ventral surface near the anterior end; near the mouth parts is a swelling on each ventrolateral surface of each thoracic somite and of abdominal somite I. Trophothylax well developed. Segmentation distinct. Spiracles small, the mesothoracic the largest. Spinules present on the lining of the trophothylax. Body hairs numerous and uniformly distributed, except none on or near the trophothylax. Of three types: (1) simple, minute to small, generally distributed; (2) simple, moderately long, a few of the longest on each ventrolateral surface of a few abdominal somites; (3) with tortuous shaft and one ²⁻⁶ apical hook, 2-6 in a transverse row across the dorsal surface of each thoracic somite and each abdominal somite I-IV. Cranium broader than long. Antennae minute. Head hairs moderately numerous, simple, minute to short. Labrum small, broader than long; posterior surface spinulose. Mandibles rather small; ratio of head width to mandible length 2.6-4.9 (average 3.3); ratio of mandible length to mandible width 1.7-2.5 (average 2.1); apex stout and round-pointed; with some part of the surface spinulose. Maxillae with some part of the surface spinulose. Labium small, with a few short arcuate rows of spinules near the hypopharynx; palp a cluster of five sensilla. Hypopharynx densely spinulose.

Creighton, 1950:—"The head of the pseudomyrmecine larva is quadrate in shape and larger than that of other ant larvae. Beneath it lies a cluster of papillae (the exudatoria) which arise from the thoracic and the first abdominal segments. Between these papillae the first abdominal segment is expanded into a sort of a shelf or pocket (the trophothylax) that underlies the mouth of the larva. Food is placed in this pocket by the workers. This food is of a very unusual sort. It consists of bits of tissue which have collected in the infrabuccal pocket of the

worker and from which most of the juices have been sucked by the worker before it is deposited on the trophothylax of the larva. The deposited pellet is, therefore, rather firm and dry, and not available for immediate ingestion by the larva. But the larva proceeds to rectify this matter by grinding the pellet between two opposable plates (the trophorinium) [sic] which are covered with very fine striae. After the pellet has been finely comminuted the fragments are swallowed. It is presumed that this process of comminution not only makes it possible for the larva to swallow the pellet but also releases particles of food which had escaped digestion in the infrabuccal pocket of the worker. It may be added that in all other ants except the Pseudomyrmecinae the contents of the infrabuccal pocket are regularly discarded" (pp. 78-79).

Emery, 1899:—"Questi due generi offrono un tipo di larve tutto speciale. Ho esaminato quelle della *Pseudomyrma flavidula* F. Sm. [= *palidus*] (Caienna, racc. da Pillault) e di alcune *Sima* [= *Tetraponera*], particolarmente delle *S. natalensis* F. Sm. e *S. clypeata* Emery (Colonia del Capo, racc. del Dr. Brauns). Le larve sono subcilindriche nella parte anteriore e alquanto assottigliate indietro; i primi segmenti postcefalici sono più sviluppati nella parte dorsale, accorciati nella parte ventrale, per cui, sul profilo, appaiono come disposti a ventaglio, il loro contorno dorsale formando complessivamente una curva o gobba che costituisce l'estremità anteriore apparente della larva, mentre il capo, ossia l'estremità anteriore morfologica trovasi collocato sulla faccia ventrale del corpo. Perciò queste larve possono dirsi *ipocefale*, a differenza di quelle del maggior numero delle altre formiche, che diremo *ortocefale*. Nelle *Sima* il capo è depresso e non sporge quasi per nulla dalla superficie ventrale della larva, la sua estremità boccale essendo ricevuta, allo stato di riposo, in un incavo del 3° e 4° segmento del tronco su cui poggia. Nella *Pseudomyrma*, il capo è rotondeggiante e distintamente sporgente, e i segmenti 3° e 4° del tronco non sono incavati per riceverlo. Le mascelle non hanno sporgenze coniche; al loro posto si trovano dei gruppi di piccoli tubercoli; due simili gruppi si osservano sul labbro inferiore, e anche qui mancano i coni. Le mandibole sono piccole, poco sporgenti, ma robuste e bidentate all'apice. Carattere affatto proprio delle larve di *Sima* e *Pseudomyrma* è la presenza di un paio di piccole appendici del capo che considero come rudimenti di antenne.³ Ciascuna di esse consiste di due piccole sporgenze ineguali, coniche o subcilindriche, terminate da un pelo ottuso minutissimo (pelo olfattivo?). I peli del corpo sono brevi e semplici, però si osservano, distribuite lungo il corpo, quattro doppie serie di lunghe setole uncinatate all'apice

³For many years this subfamily has been called Pseudomyrmecinae; the type genus was called *Pseudomyrma*. See M. R. Smith, 1932, Proc. Entom. Soc. Wash. 54: 97-98.

⁴This was apparently the first time the antennal rudiments in ant larvae were recognized and named.

e regolarmente disposte sui singoli segmenti" (pp. 6-7).

"Quello delle *Sima* e *Pseudomyrma* che, oltre alla ipocefalia estremamente sviluppata, offrono un carattere specialissimo nella presenza di rudimenti delle antenne. Credo che questo fatto molto notevole, unitamente, ai caratteri particolari ben noti del capo dell'immagine, giustificherà la separazione di questi generi dal resto delle Myrmicinae, formandone una nuova sottofamiglia delle *Pseudomyrmecinae*. [This paragraph translated by Wheeler, 1920, p. 47.]

"Soltanto l'esame di serie più complete di larve permetterà di riconoscere se la struttura del loro corpo, e specialmente quella delle parti boccali e dei peli e l'ordinamento di questi presentino caratteri capaci di servire a fondare su più solide basi e a migliorare la classificazione tuttavia incerta della sottofamiglia delle Myrmicinae" (p. 8).

Emery, 1921, p. 21:—"Larves hypocéphales."

Forel, 1922, p. 136:—"Les larves . . . sont nourries avec le contenu du sac buccal de leurs \varnothing , avec ou sans addition de proies fraîches dépecées. Les *Pseudomyrmini* qui habitent les épines d'acacia se nourrissent aussi des corpuscules dits de Belt, produits par leur acacias." [=1928, Vol. I, p. 516: "The larvae . . . are fed with the contents of the buccal sac of their \varnothing , with or without the addition of freshly-quartered prey. The *Pseudomyrmini* which inhabit acacia spines feed also on the 'Beltian bodies' produced by their acacias."]

Imms (1931, pp. 62-63) discussed briefly exudatoria, trophallaxis and trophothylax.

Wheeler, 1918, p. 313, footnote:—"It would seem . . . that the exudatoria must be regarded as coenogenetic, or new formations peculiar to the young larvae of certain Old World genera of *Pseudomyrmini*."

Wheeler, 1920, pp. 47-48 gives a brief review of his 1918 paper and a preview of Wheeler and Bailey, 1920, and translates a brief portion of Emery's 1899 description. The *trophorhinium* is defined on page 48.

Wheeler and Bailey, 1920:—"The adult larvae of all four genera of *Pseudomyrmecinae* are much alike. The body is long, straight and cylindrical, not broader posteriorly as in nearly all other ant-larvae. The anterior and posterior extremities are blunt and rounded and the segments are all sharply defined. The integument is uniformly thin and perfectly transparent, though tough, only the mandibles, as a rule, being strongly chitinated and the lining of the buccal cavity somewhat pigmented. The prothoracic segment is large and hood-shaped,⁹ and in certain species

can be drawn down over the head; the meso- and metathoracic segments are narrowed ventrally, the head is large, somewhat flattened, usually subrectangular, about as broad as long and embedded in the ventral portions of the thoracic segments. The antennal rudiments are always distinct as small, rounded papillae, each bearing three sensillae. The mandibles are small, stout and bidentate, sometimes with a vestige of a third tooth, their upper surfaces covered with regular rows of subimbricate papillae. The maxillae are large, swollen and rounded, lobuliform, the labium short and broad, with the transverse, slit-shaped opening of the salivary duct in the middle. The sensory organs which in many other ants have the form of papillae or pegs on the maxillae and labium are in the *Pseudomyrmecinae* usually reduced to small areas or feeble eminences, bearing the groups of sensillae. The anterior maxillary organ has five, the posterior two and each labial organ has five of these sensillae. The buccal cavity is broad and transverse, its dorsal and ventral walls being in contact and both furnished with fine, regular transverse ridges. This peculiar structure, the *trophorhinium*, will be described in greater detail below. Each thoracic segment bears a rounded papilliform exudatorium ventrally on each side next to the head. The sternal portion of the first abdominal segment is transversely elliptical, swollen, protuberant and furnished with a food-pouch, the *trophothylax*, opening forward, i.e., toward the mouth-parts. The hairs on the body of the larva are of three kinds: first, short, stiff, very acute hairs, generally and rather evenly distributed over the whole surface (*microchaetae*); second, much longer, stouter, more gradually tapering, lash-like and somewhat curved hairs of unequal length, singly or in a row or loose cluster on each ventrolateral surface of each abdominal segment (*acrochaetae*), and third, long hairs, of uniform length, only slightly tapering, with hooked tips (*oncochaetae*). These are normally present in transverse rows of four to eight on the dorsal surfaces of the three thoracic and first three to eight abdominal segments. On the more posterior segments they are often represented by simple, i.e., pointed hairs. [The preceding quoted by Wheeler 1922a, pp. 103-104.] In the genera *Tetraponera*, *Vitilicola* and *Pseudomyrma* the youngest larvae, apart from their proportionally longer and more conspicuous *oncochaetae* and *acrochaetae* and more protuberant *trophothylax*, have essentially the same structure as full-grown individuals. In the two species of *Pachysima*, however, . . . the youngest larvae are very unusual in possessing long, stout, blunt bristles in the place of the *oncochaetae* and extraordinary exudatoria which may have the form of appendages on the three thoracic and first abdominal segments" (pp. 256-258).

"The pellets of the various *Pseudomyrmecinae* . . .

⁹Wheeler frequently referred to the hood formed by the prothorax, but it apparently is not a permanent structure and is only present when the larva has its head retracted, i. e., "imbedded in the ventral portion of the thoracic segments".

show considerable uniformity in nearly all the species and considerable diversity in the individual pellet. In other words, all the species supply their larvae with both insect and vegetable substances, but of many different kinds. There can be no doubt that small miscellaneous insects furnish the most important ingredient of the pellets in most species, and that this ingredient, which supplies the most easily assimilable proteins for the growth of the larvae, is rarely completely lacking even in the acacia-inhabiting species. In the latter the Beltian bodies are unquestionably important sources of food for both the adults and the young. Nor would the spores, hyphae and pollen grains, which are in most cases at least merely strigil-sweepings, be so constantly fed to the larvae, unless they could be at least partly utilized as food. That these ingredients, and especially the spores and pollen, contain substances of high nutritive value, is certain, and it is not improbable that the larvae can triturate them by means of the trophorhinium and thus render them assimilable. This must, indeed, be true, if the spores are actually ingested, for none of them can be detected as whole bodies among the stomach contents as is the case in the . . . Myrmicinae (*Leptothorax*, *Cryptocerus* and *Catalacus*), which have no trophorhinium and swallow entire insect fragments and spores . . .

"The trophorhinium, an organ apparently overlooked by previous observers, is beautifully developed in all the Pseudomyrmacinae, but seems to show little variation within the subfamily. As stated above, it consists of numerous transverse, parallel, very minutely spinulose ridges in the chitinous cuticle lining the flattened mouth-cavity. If the mouth be carefully opened with the dissecting needles and the dorsal and ventral portions spread apart it will be seen that the dorsal surface or portion, corresponding anteriorly to the ventral surface of the labrum, begins near its anterior border and extends back nearly to the opening of the gullet. The more anterior ridges are made up of rather arcuate sections, whereas the posterior are straight and more even. The ventral surface or portion, corresponding to the floor of the mouth, is of similar structure, except that the ridges are much more numerous and closer together, especially anteriorly. Posteriorly, in the neighborhood of the gullet, they are interrupted and much further apart. On both surfaces the very fine, hair-like spinules point towards the oral orifice. The cuticle of both surfaces is slightly darker than elsewhere on the body. It is not necessary, however, to separate the walls of the buccal cavity in order to determine the peculiarities of the two surfaces. This can be done very readily by focussing with the fine adjustment of the microscope on the head of a larva from which all the soft parts have been removed by treat-

ment with caustic potash, or by the study of sections. Here the difference in spacing between the fine ridges of the dorsal and ventral surfaces is distinctly seen, the latter beginning just behind the orifice of the salivary duct on the labium and the former extending further forward on the ventral surface of the labrum.

"That an organ of such structure would be admirably adapted to triturating particles of food and sifting or straining out the coarser and harder pieces seems to us to be extremely probable. The process of feeding would appear to be as follows: The pellet placed in the trophothylax by the worker nurse and consisting of the strigil-sweepings, etc. taken from her own infra-buccal pocket *plus* some fragments of insect prey, is probably bathed or saturated with the saliva of the larva secreted into the trophothylax from the orifice of the labial duct. The proteolytic ferment of the secretion would evidently peptonize the softer portions of the particles which could then be drawn back by the mandibles in installments between the two surfaces of the trophorhinium where the indigestible chitinous fragments could be separated out and the remainder turned over to the gullet and swallowed. As a matter of fact, the senior author has seen numerous particles, like those in the trophothylax, spread out between the two apposed surfaces of the trophorhinium in some larvae that had been suddenly killed by immersion in strong alcohol while apparently in the very act of feeding" (pp. 266-268). The "delicate transverse ridges [of the trophorhinium] have developed from the minutely granular or reticular structure so characteristic of the general chitinous integument" (p. 268). "When the mandibles are opened or closed, their imbricated surfaces would naturally rub against the dorsal plate of the trophorhinium. . . Not improbably, therefore, the rough surfaces of the mandibles may reinforce the triturating and sifting functions of the trophorhinium. All of these structures, however, seem to have still another function. Comparison of the trophorhinium with the stridulatory organs at the base of the mid-dorsal aspect of the post-petiole and first gastric segment in adult ants . . . suggests that it may also have a sound-producing function, when it is not being used as a mill or strainer and the two apposed surfaces can be rubbed directly against one another, *i.e.*, without the intervention of food particles. Owing to the small size of the organ and the extreme delicacy of its parallel ridges, the tones produced would be very feeble and of very high pitch" (p. 269).

Wheeler (1928) briefly mentioned the trophothylax (pp. 200-201=1926, pp. 240-242) and exudatoria (p. 234=1926, pp. 281-282). "The youngest larvae, till their jaws are strong enough to triturate the pellets, are fed on saliva, and perhaps the same substance may also be given

to some of the older larvae and determine their development as queens, but of this there is no evidence" (p. 201 = 1926, p. 242).

Genus *Pseudomyrmex*¹⁰ Lund

Body straight, subcylindrical, outline slipper-shaped or parallel-sided; anterior end more broadly rounded than the posterior end; head applied to the ventral surface near the anterior end; near the mouth parts is a swelling on each ventrolateral surface of each thoracic somite and of abdominal somite I. Trophophylax well developed. Segmentation distinct. Some part of the integument spinulose. Body hairs numerous and uniformly distributed (except none on or near the trophophylax). Of three types: (1) simple, minute to short, on all somites; (2) sparse, simple, short to moderately long, with a few of the longest on each ventrolateral surface of a few of the abdominal somites; (3) with tortuous shaft and one apical hook, 2-6 in a row across the dorsal surface of each thoracic somite and a few anterior abdominal somites. Cranium broader than long. Antennae minute. Head hairs moderately numerous, simple, minute to short. Labrum small, with the ventral corners rounded and with a median ventral projection; anterior surface usually without hairs but with about 14 sensilla and a few rows of spinules; ventral border sparsely spinulose; posterior surface with about 14 sensilla and with rows of spinules. Mandible rather small, with denticles on the medial border and with some part of the surface spinulose. Maxilla prominent, swollen ventrolaterally, the apex directed medially, digitiform or paraboloidal and with a few short arcuate rows of spinules; palps and galeae represented by clusters of sensilla. Labium small, short and rounded, with a few short rows of spinules dorsally; palp represented by a cluster of five sensilla.

Escherich, 1906:—"Tonnenförmige [Larven], welche in der Mitte am dicksten sind und nach beiden Enden gleichmässig sich verjüngen (*Sima* [= *Tetraponera*], *Pseudomyrma* [= *Pseudomyrmex*])." Der Kopf ist "bauchwärts eingeschlagen, so dass die Mundöffnung nach hinten gerichtet ist ('hypognath Typus')." (pp. 73-74 = 1917, p. 95). "Antennen fehlen meistens vollkommen, nur bei wenigen Larven (*Sima*, *Pseudomyrma*) sind winzige Fühlerrudimente festgestellt worden" (p. 75 = 1917, p. 95). "... während die extrem hypognathen Larven (wie z. B. *Sima*) ausschliesslich auf flüssige Nahrung angewiesen sein dürften" (p. 76 = 1917, p. 98).

Pseudomyrmex alliodorae Wheeler

Pl. I, figs. 1-17; Pl. II, figs. 1 and 4-8

Mature Worker Larva: Length (through

spiracles) about 3.6 mm. Straight length about 3.5 mm. Body straight, subcylindrical, outline vaguely slipper-shaped in both ventral and lateral views; anterior end formed from the dorsal surface of the prothorax; slightly constricted at abdominal somite II; widest at abdominal somite IV; head applied to the ventral surface near the anterior end; near the mouth parts is a swelling on each ventrolateral surface of each thoracic somite and of abdominal somite I; narrowed toward the posterior end which is round-pointed. Anus subterminal. Gonopod vestiges present. Segmentation distinct. Trophophylax well developed. Spiracles small, diameter decreasing slightly posteriorly. Integument of ventral surface of thorax and of abdominal somites I and II (i.e., the lining of the trophophylax) spinulose, the spinules in numerous short transverse rows. Body hairs numerous and uniformly distributed, except on the trophophylax and areas adjacent to it. Of three types: (1) on all somites, simple, minute to short (0.009-0.018 mm.), without alveolus and articular membrane, the most numerous type; (2) simple, short to moderately long (0.018-0.18 mm.); two of the longest on each lateral surface of each abdominal somite III-V; moderately long (about 0.045 mm.) hairs replace the single-hooked hairs on abdominal somites V-IX; a few of the shortest on every somite; (3) with sigmoidal flexure and a single apical hook, about 0.144 mm. long, four in a row across the dorsum of each thoracic somite and each abdominal somite I-IV. Cranium vaguely subhexagonal in anterior view, but with rounded corners. Head hairs simple, moderately numerous (about 80), minute to short (0.009-0.036 mm.). Antennae minute, each a slight elevation with three sensilla, each of which bears a spinule. Labrum small, breadth 1.3 times the length; ventrolateral corners broadly rounded; with a small median ventral projection; each half of anterior surface with 6-8 sensilla, some of which are near the ventral border; anterior surface with short arcuate rows of spinules on and near the ventral border; posterior surface spinulose, the spinules in transverse rows dorsally and in short arcuate rows ventrolaterally; posterior surface with seven sensilla on each half. Mandible rather small; apical half heavily sclerotized; subtriangular in lateral view; with one stout round-pointed apical tooth, which is curved posteriorly and one or two rounded medial teeth; near the middle of the anteromedial surface are several denticles in a few oblique rows. Maxilla swollen ventrolaterally, with the digitiform or paraboloidal apex directed medially; with a patch of spinules in arcuate rows on the apical and medial surfaces; palp represented by a slightly raised cluster of five sensilla (three small and bearing a spinule each, one large and one small and encapsulated); galea represented by two sensilla. Labium small in anterior view,

¹⁰We wish to thank Dr. W. L. Brown for many identifications in this genus.

with a few short arcuate rows of spinules dorsally; palp similar to maxillary palp; opening of the sericteries a short transverse slit. Hypopharynx densely spinulose, the spinules minute and in numerous subtransverse rows.

First-Instar Larva: Straight length about 0.77 mm. (Egg 0.61 mm. long.) Diameter greatest at the anterior end, diminishing gradually posteriorly. A slight invagination between the meta-thorax and abdominal somite I. Segmentation distinct. Head anteroventral. Body hairs scarce. Of two types: (1) simple, minute (0.009-0.036 mm. long), few; (2) with flexuous shaft and a single apical hook, four in a row across the dorsal surface of each thoracic somite and each abdominal somite I and II, about 0.078 mm. long, very slender. Head relatively very large. Head hairs few and minute (about 0.009 mm. long). Mandibles only feebly sclerotized, each with two small apical denticles and a patch of spinules on the medial surface. The other mouth parts appear short and rounded but otherwise very similar to those of the mature larva.

Young Larva: Straight length about 0.9 mm. Head more ventral than on first-instar larva. Mandibles feebly sclerotized; each with two straight sharp-pointed apical teeth. Maxillae with shorter apex. Otherwise, very similar to the mature larva.

Sexual Larva: Length (through spiracles) about 3.8 mm. Straight length about 3.6 mm. Very similar to worker larva except in the following details: Body not constricted. Segmentation indistinct. Body hairs slightly longer. Cranium transversely subelliptical.

Material studied: Numerous larvae from the Panama Canal Zone, G. C. Wheeler No. 265, 273 and 278.

Pseudomyrmex apache Creighton

Straight length about 5.9 mm. Similar to *alliodorae*, except as follows: Body long, slender and subovoid; widest at abdominal somites V and VI, tapering rapidly to the posterior end which is narrowly rounded. Body hairs: (1) 0.006-0.018 mm.; (2) 0.027-0.25 mm., one of the longest on each ventrolateral surface of each abdominal somite II-VI (two or three prominent hairs on each ventrolateral surface of abdominal somites IV and V); (3) 0.185-0.25 mm., two or three on each dorsolateral surface of each thoracic somite and of each abdominal somite I-IV. Labrum with 1-3 hairs and 7 or 8 sensilla on each half of the anterior surface. Mandible with one apical and two medial teeth; anterior surface with rather numerous large isolated spinules. (Material studied: numerous larvae from Mexico and Texas, collected by W. S. Creighton.)

Pseudomyrmex belti Emery

Apparently similar to *alliodorae* except in the following details: Body hairs: (1) 0.009-0.027

mm. long; (2) more numerous and 0.036-0.33 mm. long; (3) about 0.27 mm. long and six (sometimes five) per somite, without a flexure (i.e., with a curved shaft). Head with a slight elevation above each antenna. Head hairs less than half as numerous (about 30). Labrum twice as broad as long. Mandible with a distinct apical and one subapical tooth. (Material studied: integuments of the anterior ends of six larvae from Mexico labelled "*Ps. belti fulvescens*.")

Safford (1923) has a photograph. (Pl. 3) of ants, larvae and pupae taken from an acacia thorn from Tampico, Mexico (labelled "*var. fulvescens*").

Wheeler and Bailey, 1920:—"Oncochaetae six on pro- and mesothorax, three on each side of the middorsal line. Acrochaetae three or four on each side of the abdominal segments, in a transverse row. Microchaetae sparse as in *filiformis* but coarser and more conspicuous" (p. 259, referred to "*var. fulvescens*").

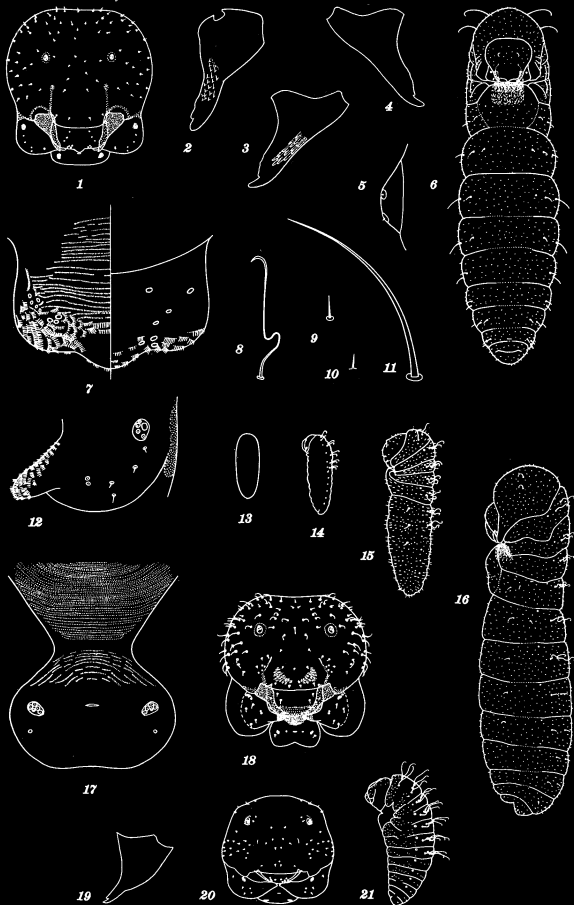
"*Pseudomyrmex belti* (32 pellets).—In the pellets of this ant, which is an obligatory inhabitant of the thorns of the bull-horn acacias, insect fragments are less abundant than in the various preceding species; spores are also scarce in most cases; pollen grains much more abundant. In nearly all cases pieces of Beltian bodies, with occasional bits of other vegetable tissues, are present" (pp. 263-264). Pl. figs. 9 and 38 photomicrographs of parts of larval pellets.

"*Pseudomyrmex belti* var. *fulvescens* (21 pellets).—Since the habits of this variety are the same as those of the typical *belti*, it is not surprising to find essentially the same constituents in the trophophylax pellets. There are, however, in addition to the sparse bits of insects, spores, pollen-grains and fragments of Beltian bodies, numerous plant-hairs and bits of miscellaneous vegetable tissues. In a few of the pellets the pollen is largely that of pines. In a series of larvae taken from acacia thorns in the dry Zacapa region of Guatemala no insect fragments

EXPLANATION OF PLATE I

Pseudomyrmex alliodorae Wheeler, Figs. 1-17.—1, head in anterior view, X96; 2, left mandible in anterior view, X278; 3, left mandible in medial view, X278; 4, left mandible in lateral view, X278; 5, left antenna in lateral view, X556; 6, mature larva in ventral view, X28; 7, labrum (left half of drawing shows posterior view, right half anterior), X353; 8, single-hooked body hair, X278; 9 and 11, simple body hairs, X278; 10, simple body hair without alveolus and articular membrane, X278; 12, left maxilla in anterior view, X278; 13, egg, X28; 14, first-instar larva in side view, X28; 15, young larva in side view, X28; 16, mature larva in side view, X28; 17, labium and hypopharynx in anterior view, X278.

Pseudomyrmex gracilis mexicanus Roger, Figs. 18-21.—18, head of mature larva in anterior view, X45; 19, mandible of very young larva in anterior view, X278; 20, head of very young larva in anterior view, X96; 21, very young larva in side view, X28.



were found and nearly all the pellets contain some pine pollen" (p. 264).

***Pseudomyrmex brunneus*¹ F. Smith**

Pl. II, figs. 2; text fig. 1, G and H

Straight length about 4 mm. Very similar to *alliodorae* except in the following details: Body appears much straighter, slenderer and more nearly cylindrical. Segmentation less distinct. Only one long hair on each ventrolateral surface of each abdominal somite III-VII; only two single-hooked hairs on the dorsal surface of each thoracic somite and each abdominal somite I-IV. Labrum about twice as broad as long. Mandibles smaller. Labium with the spinules more prominent and in more numerous rows. (Material studied: numerous larvae from Georgia, Paul B. Kownowski No. 926 and 944.)

***Pseudomyrmex caroli* Forel**

Apparently very similar to *alliodorae* except in the following minor details: Body hairs (1) all minute (about 0.009 mm.); (2) only one of the longest hairs on each ventrolateral surface of abdominal somites III and IV; (3) two only on the first thoracic somite. Head hairs less numerous (about 46). Labrum about twice as broad as long. Mandible with the subapical tooth narrower, the denticles more numerous. (Material studied: five flattened integuments from Guatemala.)

Wheeler and Bailey, 1920;—"Oncochaetae on all the thoracic and first to fifth abdominal segments. Acrochaetae single. Microchaetae very small and delicate so that the integument seems to be very smooth" (p. 259).

***Pseudomyrmex championi* Forel**

Apparently very similar to *alliodorae* except in the following minor details: Body hairs (1) 0.009-0.036 mm. long; (2) 0.036-0.306 mm. long, one of the longest on each ventrolateral surface of each abdominal somite III-VII; (3) about 0.31 mm. long. Head hairs 0.018-0.054 mm. long. Labrum about twice as broad as long, with two hairs on the anterior surface. Mandible with the subapical tooth more prominent. Labium with an isolated sensillum between each palp and the opening of the sericteries. (Material studied: five flattened integuments from Guatemala.)

Wheeler and Bailey, 1920;—"Oncochaetae delicate, present on three thoracic and first to fourth abdominal segments. Acrochaetae slender, single, on first to sixth abdominal segments. Micro-

chaetae small, inconspicuous" (p. 260). "One of the pellets contains a crushed insect, a 5-toothed mandible of which is left intact, together with numerous spores and pollen grains. The other pellet consists in great part of spores and pollen, with some soft material of unknown origin" (p. 264). Pl. fig. 25, photomicrograph of a portion of a larval pellet showing fragments of insects, spores and pollen.

***Pseudomyrmex decipiens* Forel**

Apparently very similar to *alliodorae* except in the following details: Body hairs (1) 0.009-0.027 mm. long; (2) 0.027-0.126 mm. long, one of the longest on each ventrolateral surface of each abdominal somite II-VI. Head hairs a little more numerous (about 95). Labrum about twice as broad as long, with two hairs on the anterior surface. Mandibles with the teeth narrow-pointed. (Material studied: nine flattened integuments from Costa Rica.)

Wheeler and Bailey, 1920;—"Very similar to *championi*, but the oncochaetae even more delicate and the acrochaetae longer and stouter. Antennal rudiments and maxillary sense-organs larger and more heavily chitinated" (p. 260). The pellets contained insect fragments, spores, pollen grains and bits of hyphae (pp. 264-265). Pl. fig. 39, photomicrograph of a portion of a pellet.

***Pseudomyrmex elegans* F. Smith**

Wheeler and Bailey, 1920;—"Antennal rudiments small. Exudatoria, especially of the prothorax, larger than in the other species. Oncochaetae long and moderately stout, on the three thoracic and first to fifth abdominal segments. Acrochaetae long, four or five in a regular transverse row on each side of all the abdominal segments. In the young larvae these hairs are very long and form an uninterrupted transverse row on the ventral and lateral surfaces of each abdominal segment" (p. 260). "Only

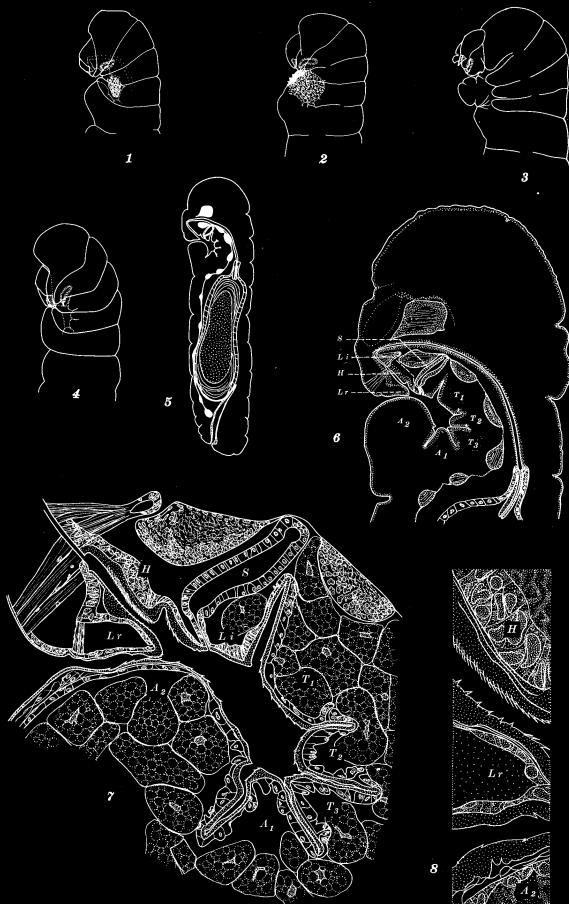
EXPLANATION OF PLATE II

Pseudomyrmex alliodorae Wheeler, Figs. 1 and 4-8.—1, phantom side view of anterior end of larva with trophothylax half full, X28; 4, phantom side view of anterior end of larva with empty trophothylax, X28; 5, sagittal section of mature larva, X28; 6, sagittal section of anterior end of larva, X82; 7, sagittal section of mouth region and trophothylax enlarged from Figure 6, X278; 8, sagittal section of hypopharynx and labrum enlarged from Figure 7 to show spinules, X814. A₁ and A₂, first and second abdominal somites; H, hypopharynx; Li, labium; Lr, labrum; S, sericteries; T₁, T₂, T₃, thoracic somites. Figs. 5-8 are from sections prepared by Donald A. Sather.

Pseudomyrmex brunneus F. Smith, Fig. 2, phantom side view of anterior end of larva with full trophothylax, X28.

Pseudomyrmex gracilis mexicanus Roger, Fig. 3, side view of anterior end of larva with trophothylax everted, X28.

¹The old generic name *Pseudomyrma* was evidently considered to be feminine. But *Pseudomyrmex* is masculine; hence all adjectival trivial names ending in -a should be changed to end in -us. Confusion will be compounded by *spinicola* which is a masculine noun in apposition with the generic name; hence its -a ending must be retained.



two pellets were obtained from a small number of larvae of this species collected by Mr. Emerson in British Guiana in an earthen termitarium. One contains considerable fragments of a small larva (apparently a Myrmeleonid, judging from a nearly entire eye), a few fungus spores, Lepidopteran scales and pieces of algal filaments. The other, much less voluminous pellet contains bits of an unidentified insect, with small pieces of vegetable tissue (bits of moss leaves?). In neither pellet was there anything that could be identified as pieces of termites or of their eggs" (p. 263).

***Pseudomyrmex elongatus* Mayr**

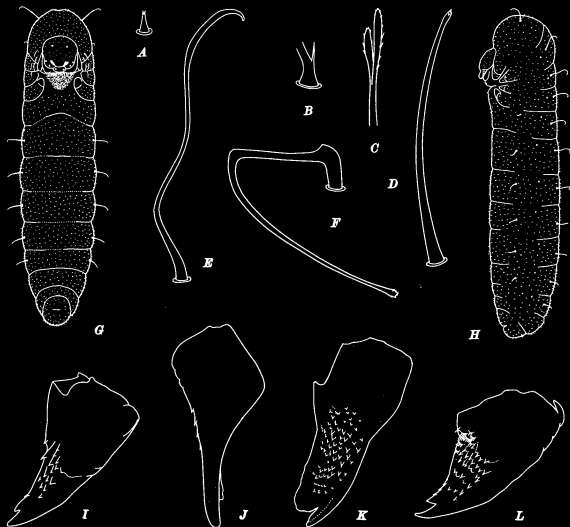
Apparently very similar to *alliodorae* except

in the following details: Body hairs (2) 0.027–0.198 mm. long, longest hairs may be present on abdominal somites III–V or III–VII; (3) about 0.18 mm. long. Head hairs fewer (about 64). (Material studied: 10 flattened integuments from Cuba.)

Wheeler and Bailey, 1920:—"Pilosity very much as in *gracilis*. Acrochaetae long, delicate, single. Microchaetae short and sparse" (p. 260). Pellets contained insect fragments, entire mites, fungus spores and hyphae and pollen grains (p. 265).

***Pseudomyrmex filiformis* (Fabricius)**

Probably similar to *alliodorae* but differing in at least these details: Head hairs fewer (about



TEXT FIG. 1

Pseudomyrmex sp. No. 285, FIGS. A–F and L.—A, very short type 2 body hair, X556; B, aberrant base of type 2 body hair, X278; C, aberrant tip of type 2 body hair, X556; D and F, two type 2 body hairs, X278; E, type 3 body hair, X278; L, left mandible in anterior view, X278.

Pseudomyrmex brunneus F. Smith, FIGS. G and H.—G, larva in ventral view, X22; H, larva in side view, X22.

Pseudomyrmex triplarinus (Weddell), FIGS. I–K.—I, left mandible in medial view, X278; J, left mandible in side view, X278; K, left mandible in anterior view, X278.

72) and 0.018-0.054 mm. long. Antennae each a hemisphere bearing three sensilla, with a small spinule each. Labrum 1.5 times as broad as long. Mandibles each with one apical and two medial teeth. (Material studied: anterior portions of seven integuments without body hairs from Guatemala.)

Wheeler and Bailey, 1920:—"Oncochaetae lacking on prothorax, rather short and delicate on the meso- and metathorax and basal abdominal segments. Acrochaetae single, not very stout. Microchaetae rather long, sparser than in *gracilis*" (p. 259). Pellets contained insect fragments, fungus spores and occasionally pollen grains and plant parenchyma (p. 264). Pl. fig. 24, photomicrograph of a portion of a larval pellet.

Pseudomyrmex godmani Forel

Straight length about 6.2 mm. Apparently similar to *alliodorae* except in the following: Body hairs (1) about 0.018 mm. long; (2) 0.036-0.3 mm. long, two to ten in a cluster on each ventrolateral surface of the metathorax and each abdominal somite I-VIII; (3) apparently four on the prothorax and six on the mesothorax, metathorax and each abdominal somite I-IV (hair bases only, no complete hairs on our specimens). Antennae each a frustum. Mandibles shorter and wider. Anterior surface of labium with an isolated sensillum between each palp and the opening of the sericteries. (Material studied: a dozen larvae from Frijoles, Panama Canal Zone, G. C. Wheeler No. 82.)

Pseudomyrmex gracilis (Fabricius)

Mature Worker Larva: Straight length about 6 mm. Similar to *alliodorae* except as follows: Body plumper. Spiracles on the mesothorax, metathorax and abdominal somite I about equal in diameter; the others decreasing slightly posteriorly. Body hairs: (1) about 0.006 mm. long and very stout at the base; (2) 0.018-0.31 mm. long, one or two of the longest on each ventrolateral surface of each abdominal somite II-VIII; (3) highly variable, four or six (but sometimes only two), about 0.32 mm. long, usually on the metathorax (but sometimes also on mesothorax or on prothorax and mesothorax) and abdominal somites I-IV. Cranium with the dorsal border feebly impressed. Head hairs shorter (0.006-0.018 mm.) and fewer (about 66). Antennae each mounted on a distinct elevation. Labrum a little more than twice as broad as long. Mandibles each with a distinct subapical tooth.

Sexual Larva: Straight length about 7 mm. Apparently very similar to the worker larva except that the body is slenderer and the head smaller; head hairs longer (0.009-0.036 mm.), with the tip sometimes curved; mandibles very small (relative to the width of the head), each with apical tooth short and rounded, medial border with three short rounded denticles.

Material studied: numerous larvae from the Panama Canal Zone (G. C. Wheeler No. 266, 271 and 276) and from Guatemala.

Donisthorpe (1921) repeated (as Figs. 1, 2 and 4) part of Figs. 3, 4A and 5, Wheeler and Bailey, 1920.

Eidmann, 1936, p. 38:—"Die langen, hakenförmigen Rückenhaare der Larven (Oncochaetae) dienen zweifellos zum Befestigen derselben an den steilen Wänden ihrer Röhrenester."

Safford (1923) used Wheeler and Bailey, Fig. 3 as Fig. 7 on p. 394.

G. C. Wheeler, 1938, Plate 16, fig. 10, shows vestigial gonopods.

Wheeler and Bailey, 1920:—"Ps. *gracilis* and varieties—Oncochaetae occasionally lacking on the pro- and mesothorax, but usually present on all the thoracic and four basal abdominal segments, replaced by simple bristles on the three succeeding segments. Acrochaetae single on first abdominal, two on second to fifth segments, the more ventral, hair smaller. Microchaetae acute, bristle-like" (p. 259). Larval pellets from colonies inhabiting dead twigs comprised bits of insects, spores, hyphae and pieces of plant tissue; those from acacia thorns lacked insect material but contained Beltian bodies, spores and a few pollen grains (p. 262). Larval pellets of "var. *dimidiata*" and "var. nov." contained insect fragments and usually spores and pollen grains (p. 263). Fig. 3 on p. 256, a larva in ventral and side views; Fig. 4A on p. 257, head and trophothylax; Fig. 5 on p. 267, trophothorium; Pl. figs. 5, 23, 28, 31, 32 and 34, photomicrographs of portions of larval pellets.

Wheeler (1922b, Fig. 62; 1923, Fig. 62; 1926, Fig. 30; 1928, Fig. 43) used Wheeler and Bailey, 1920, Fig. 3 as A and B; repeated Fig. 4A as C; and used Fig. 6 (originally labelled *Viticicola tessmanni*) as D.

Pseudomyrmex gracilis mexicanus Roger

Pl. I, figs. 18-21; Pl. II, fig. 3

Mature Worker Larva: Straight length about 6 mm. Similar to *alliodorae* except as follows: Posterior end of body narrower. Body hairs (1) 0.009-0.027 mm. long; (2) 0.036-0.31 mm. long, two to four of the longest in a cluster on each ventrolateral surface of each abdominal somite II-VII; (3) about 0.31 mm. long, six on each thoracic and each abdominal somite I-IV. Integument with spinules on the dorsal surface of posterior abdominal somites also. Cranium with the dorsal profile concave and a slight median projection which is a continuation of a welt on the anterior surface of the head. Head hairs very numerous (about 117) and 0.009-0.09 mm. long, the longer with flexible tips. Labrum twice as broad as long; with longer spinules, those on the posterior surface in combs. Mandible with two rounded medial teeth. Maxilla with a slight constriction between the cardo and stipes; apex with longer spinules.

Young Larva: Length 1-1.25 mm. Trophothylax present. Body with the diameter greatest at abdominal somite II, decreasing gradually to the posterior end which is narrowly rounded. Spiracles on the mesothorax and metathorax about 0.006 mm. in diameter; diameter of first abdominal spiracles about 0.015 mm., others decreasing posteriorly. Body hairs (1) 0.006-0.009 mm. long, few; (2) 0.006-0.018 mm. long and fairly uniformly distributed; (3) 0.126-0.216 mm. long. Integument with coarse isolated spinules on the abdomen. Cranium suboctagonal, narrowed dorsally. Head hairs minute (about 0.003 mm. long) and half as numerous as on the mature larva. Otherwise similar to the mature larva.

Material studied: numerous larvae from Mexico, P. B. Kownowski No. 1087.

Wheeler and Bailey, 1920.—Pellets contained insect fragments, spores and occasional hyphal fragments and pollen grains (p. 262). Pl. figs. 11, 17, 22, 27, 30 and 36, photomicrographs of portions of larval pellets.

Pseudomyrmex pallidus (F. Smith)

Straight length about 4.8 mm. Similar to *alliodorae* except in the following details: Relatively slenderer; only slightly enlarged at abdominal somite V; posterior end rounded. Body hairs (1) 0.009-0.027 mm. long; (2) 0.027-0.34 mm. long, one of the longest on each ventrolateral surface of each abdominal somite III-VIII and also two on each abdominal somite VII-IX replacing the single-hooked hairs; (3) about 0.23 mm. long, two on each thoracic and on each abdominal somite I-VI. Head relatively smaller. Head hairs more numerous (about 92). Mandibles small. Labium with more numerous short rows of spinules. (Material studied: numerous larvae from Florida, P. B. Kownowski No. 766; from Mexico, V. J. Shiner; and from the Bahamas).

Eidmann, 1936, p. 39: a brief description (under the name *Ps. flavidula*) based on Wheeler and Bailey, 1920.

Emery (1899, pp. 6-7) gave a brief description of this species under the name *Ps. flavidula*; see under the subfamily above. Plate II, Fig. 8a, larva in side view; 8b, head in side view, enlarged.

Wheeler and Bailey, 1920, under *Ps. flavidula*:—"Acrochaetae flagelliform, rather delicate, single. Microchaetae sparse, distinct" (p. 260). Larval pellets contained insect fragments, fungus spores, mycelium, pollen and other plant tissue; those of "*var. delicatula*" were similar but contained also bacteria and whole mites (p. 265). Pl. figs. 4, 15, 20, 21 and 26, photomicrographs of larval pellets.

Pseudomyrmex pazosi Santschi

Straight length about 4 mm. Similar to *alliodorae* except as follows: Abdomen slenderer.

Body hairs (1) 0.009-0.027 mm. long; (2) 0.036-0.198 mm. long, one of the longest on each ventrolateral surface of abdominal somites III and IV, conspicuous but slightly shorter on abdominal somites V-VIII; (3) about 0.18 mm. long, two on each thoracic somite and on abdominal somites I-IV. Cranium appears subrectangular. Mandible with base less inflated. Maxillary palp a sclerotized slight elevation with five sensillae. Labium with more rows of spinules. Hypopharynx with long spinules. (Material studied: six larvae from Cuba, collected by E. O. Wilson.)

Pseudomyrmex rufomedius F. Smith

Wheeler and Bailey, 1920:—"Acrochaetae five or six on the side of each abdominal segment, a few smaller homostichous hairs also on the thoracic segments" (p. 259). "Nearly all the pellets contain numerous bits of insect material, some in chunks. Spores and pollen are also present, being in some cases very abundant" (p. 263). Pl. fig. 33, photomicrograph of portion of a larval pellet.

Pseudomyrmex sericeus Mayr

Straight length about 4.5 mm. Similar to *alliodorae* except in the following details: Body relatively slenderer. Body hairs: (1) 0.009-0.024 mm. long; (2) 0.024-0.25 mm. long, one of the longest on each ventrolateral surface of each abdominal somite IV-VI; (3) similar to *alliodorae*. Mandible with a larger patch of more numerous spinules. Maxilla with the cardo swollen ventrolaterally. (Material studied: numerous larvae from the Panama Canal Zone, G. C. Wheeler No. 283.)

Wheeler and Bailey, 1920:—"Oncochaetae slender, on the 3 thoracic and first to third abdominal segments. Acrochaetae stout, single, on the first to sixth abdominal segments. Microchaetae extremely short and sparse so that the integument appears to be very smooth. Hairs on head scattered and inconspicuous" (p. 260). Larval pellets contain numerous large insect fragments, fungus spores, bits of hyphae and medullary tissue (p. 264). Pl. figs. 7 and 40, photomicrographs of portions of larval pellets. This material was referred to as "*var. fortis*."

*Pseudomyrmex spinicola*¹ Emery

Wheeler and Bailey, 1920, p. 264:—"The single pellet obtained from a larva of this *Acacia*-inhabiting species defies analysis. It consists of a soft, apparently coagulated substance, possibly of vegetable origin, but no cellular elements can be detected in it."

Pseudomyrmex triplarinus (Weddell)

Text fig. 1, I-K

Mature Worker Larva: Straight length about 5.2 mm. Similar to *alliodorae* except as follows:

Diameter of spiracles on the mesothorax, metathorax and abdominal somite I subequal; diameter of others a third less and subequal. Body hairs (1) 0.009–0.012 mm. long; (2) 0.018–0.25 mm. long, one of the longest on each ventrolateral surface of each abdominal somite II–VII; (3) about 0.25 mm. long, six on each thoracic somite, four on each abdominal somite I–VIII. Whole integument with minute spinules in short transverse rows. Cranium transversely subelliptical. Head hairs 0.024–0.054 mm. long. Mandible quadrangular in anterior view, medial surface with a broad thin blade bearing numerous rather long denticles on its anterior surface.

Young Larva: Length about 3 mm. Body largest at the anterior end and tapering to a narrow posterior end. Otherwise similar to mature larva.

Material studied: numerous larvae from Panama Canal Zone, G. C. Wheeler No. 267.

G. C. Wheeler (1938, pp. 141–142) reported (under the name *Ps. arboris-sanctae symbiotica* var. *loewensohni*) the presence of vestigial gonopods on the seventh and eighth abdominal somites.

Pseudomyrmex sp.

Straight length about 5 mm. Similar to *alliodorae* except in the following details: Body hairs (1) 0.012–0.024 mm. long; (2) 0.03–0.4 mm. long, one to four of the longest on each ventrolateral surface of each abdominal somite I–VIII; (3) about 0.24 mm. long, four on each thoracic somite and on each abdominal somite I–V. Head rather small. Cranium transversely subelliptical in anterior view. Head hairs fewer (about 60), longer (0.036–0.08 mm.) and slightly curved. Antennae each a distinct knob. Labrum about twice as broad as long. (Material studied: numerous larvae from Costa Rica, G. C. Wheeler No. 18.)

Pseudomyrmex sp.

Straight length about 3.2 mm. Similar to *alliodorae* except as follows: Body relatively slender. Body hairs (1) 0.006–0.012 mm. long; (2) 0.018–0.15 mm. long, one of the longest on each ventrolateral surface of each abdominal somite III–VI; (3) about 0.15 mm. long, four on each thoracic somite and on abdominal somites I–IV (sometimes none on the prothorax). Integument of dorsal surface of posterior somites with a few short transverse rows of spinules. Labrum 1.7 times as broad as long; sometimes two hairs on anterior surface. (Material studied: two dozen larvae from Texas, W. S. Creighton No. 155.)

Pseudomyrmex sp.

Straight length about 6 mm. Similar to *alliodorae* except as follows: Body hairs (1) 0.009–0.012 mm. long, simple or with a few

denticles at the tip; (2) 0.024–0.25 mm. long, 2–12 across the ventral surface of abdominal somites I–VIII; (3) about 0.2 mm. long, four in a row across the dorsal surface of each thoracic somite and abdominal somites I–VI. Head rather small; cranium transversely subelliptical in anterior view. Head hairs less numerous (about 60) and 0.018–0.06 mm. long. Each antenna a distinct knob. Labrum 1.7 times as broad as long; with two hairs on the anterior surface. Mandible with the medial tooth subequal to the apical tooth; edge of blade erose. (Material studied: numerous larvae from Costa Rica, G. C. Wheeler No. 279.)

Pseudomyrmex sp.

Text fig. 1, A–F and L

Probably similar to *alliodorae* except as follows: Body hairs (1) apparently lacking; (2) 0.006–0.33 mm. long, about 18 of the longest across the ventral surface of abdominal somites IV–VII, straight or kinked or slightly curved, usually with a swollen tip bearing a few denticles; (3) about 0.25 mm. long, four to six on each thoracic somite and each abdominal somite I–VI. Cranium quadrangular in anterior view, with all corners rounded. Head hairs 0.012–0.018 mm. long, with multified tip. Labrum about twice as broad as long, with four hairs on the anterior surface. Mandible evenly curved from apex to base (*i.e.*, no noticeable basal swelling); with a definite subapical tooth. (Material studied: two flattened integuments from Panama, G. C. Wheeler No. 285.)

Pseudomyrmex spp.

Wheeler and Bailey, 1920, pp. 265–266:—Larval pellets from Patulul, Guatemala, contained insect fragments, spores, hyphae, pollen-grains and miscellaneous plant tissue (p. 265). Pl. fig. 35, photomicrograph of a portion of a pellet.

From Antigua, Guatemala. Larval pellets similar to above (p. 265).

From Escuintla, Guatemala. One pellet contained a few spores, the other fragments of chitin (p. 265).

From Cartago, Costa Rica. Pellets contained arthropod fragments, spores, bits of mycelium and pollen (p. 266).

Genus *Tetraponera* F. Smith

Body straight, slender and subcylindrical; head applied to ventral surface near the anterior end. Near the mouth parts is a swelling on each ventrolateral surface of each thoracic somite and of abdominal somite I. Trophothylax well developed. Segmentation distinct. No spinules seen on the integument. Body hairs numerous and rather uniformly distributed (but none on and adjacent to the trophothylax). Of three types: (1) simple, minute to short, most numerous;

(2) simple, moderately long, 2-10 on the dorsal and lateral surfaces of most somites; (3) with sinuous shaft and one apical hook, on abdominal somites I-VI. Cranium subrectangular. Antennae minute. Head hair numerous, short and simple. Labrum small, with the ventral corners rounded and the ventral border entire; anterior surface with 2-4 hairs, about 14 sensilla and a few arcuate rows of spinules; ventral border with a few spinules; posterior surface spinulose and with four sensilla. Mandible rather small; with one lateral, one apical and one blunt medial tooth. Maxilla prominent, swollen ventrolaterally; the apex directed medially, conical and with a few minute spinules; palp a slender peg with one apical, two lateral and two basal sensilla; galea represented by two sensilla. Labium short and rounded; no spinules seen; palp a cluster of five sensilla.

Emery (1899, pp. 6-8) gave a brief description of this genus. (See under the subfamily above).

Escherich (1906 and 1917) described briefly this genus. (See above under the genus *Pseudomyrex*.) Bischoff, 1927, p. 384 quoted Escherich's views on feeding.

Forel, 1922, pp. 135-136 (=1928, vol. I, pp. 515-516) gives a summary of Wheeler's work on the trophothylax, trophorhinium and feeding of *Tetraponera* (referred to as *Sima*) larvae.

Wheeler (1920, pp. 47-48), translates a small portion of Emery's 1899 description, gives a brief review of his own 1918 paper and a short preview of Wheeler and Bailey, 1920.

Wheeler, 1922a, p. 105:—"Larva hypocephalic, with papillary exudatoria on the three thoracic and first abdominal segments. Dorsal surface with long straight hairs, hooked at their tips."

Tetraponera aitkeni (Forel)

Pl. III, figs. 1-16

Mature Worker Larva: Straight length about 3.2 mm. Long, slender and subcylindrical; in ventral view only the prothorax and abdominal somites VII-X decreasing in diameter; in side view, widest at abdominal somite V, tapering slightly to both ends; posterior end narrowly rounded; anterior end broadly rounded and formed from the dorsum of the prothorax; head applied to the ventral surface near the anterior end; near the mouth parts is a swelling on each ventrolateral surface of each thoracic somite and of abdominal somite I. Trophothylax present. Anus subterminal. Segmentation distinct. Spiracles small; mesothoracic 1.5 times the metathoracic and first abdominal in diameter; the others decreasing only slightly. No spinules seen on the integument. Body hairs numerous and uniformly distributed, but none on the trophothylax and areas adjacent to it. Of three types: (1) most numerous, simple, minute to short (0.018-0.048 mm.), without alveolus and articular membrane; (2) simple, moderately long

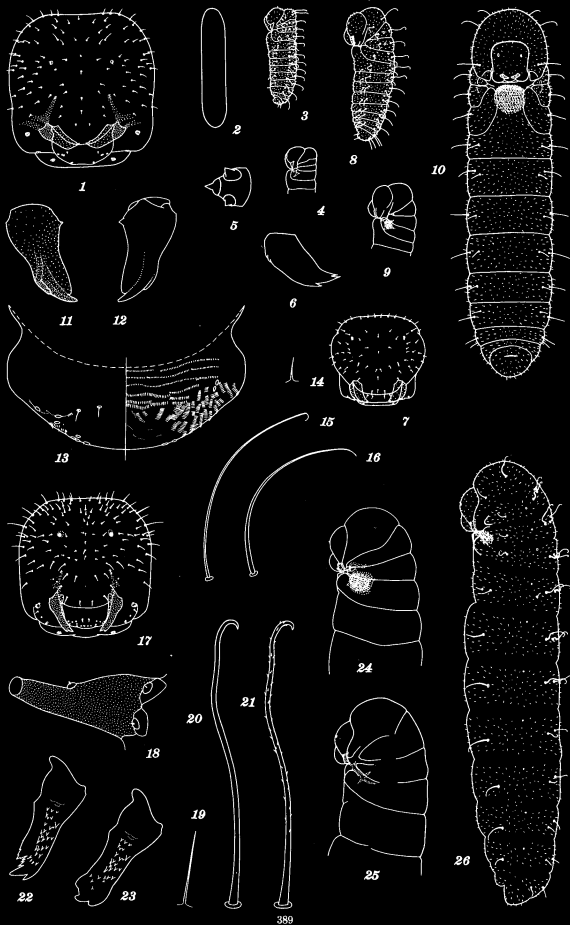
(about 0.075 mm.), six in a row around each abdominal somite VII-IX (except on the ventral surface); (3) sinuous, with a single hook, moderately long (0.068-0.2 mm.), six in a row around each thoracic somite and each abdominal somite I-VI (but not on the ventral surface). Cranium subrectangular in anterior view, with the dorsal corners rounded. Head hairs numerous (about 102), simple, short (0.01-0.05 mm.), rather uniformly distributed. Antennae minute, each a small rounded elevation with three sensilla, each of which bears a short spinule. Labrum small, short (breadth about 1.6 times length), sublunate; anterior surface with three sensilla and one or two short hairs on each half; ventral border with three sensilla on each half; anterior and ventral surfaces with very few short arcuate rows of minute spinules; posterior surface with two sensilla on each half; posterior surface with a few rows of spinules, which are subtransverse dorsally but sublongitudinal near the ventral border. Mandible rather small, somewhat curved posteriorly but only slightly medially; apex forming a small blunt tooth; a small subapical lateral tooth on the posterior surface; a median blade (variable in length), terminating in a rounded ventral projection, with or without an erose border near the apex. Maxilla swollen ventrolaterally, with the conoidal apex directed medially and bearing a few minute spinules (isolated or in short rows); palp a slender peg with one apical, two lateral and two basal sensilla; galea represented by two sensilla. Labium short and wide; palp represented by a cluster of five sensilla; opening of sericteries a short transverse slit on the ventral surface. Hypopharynx with numerous transverse rows of spinules, the rows so close together that the spinules overlap.

EXPLANATION OF PLATE III

Tetraponera aitkeni (Forel), Figs. 1-16.—1, head in anterior view, X96; 2, egg, X28; 3, first-instar larva in side view, X28; 4, phantom side view of anterior end of first-instar larva to show trophothylax, X28; 5, left antenna of first-instar larva, lateral view, X1415; 6, right mandible of first-instar larva, anterior view, X250; 7, head of first-instar larva, anterior view, X96; 8, second-instar (?) larva in side view, X28; 9, phantom side view of anterior end of second-instar (?) larva, showing food in trophothylax, X28; 10, mature larva in ventral view, X28; 11, left mandible in posterior view, X250; 12, left mandible in anterior view, X250; 13, labrum (left half of drawing shows anterior view, right half posterior view), X353; 14-16, three types of body hairs, X278.

Tetraponera allaborans Walker, Figs. 17-21.—17, head in anterior view, X83; 18, left maxillary palp in lateral view, X1000; 19, short body hair, X648; 20 and 21, single-hooked body hairs, without and with denticles, X648.

Tetraponera sp. No. 1217, Figs. 22-26.—22, left mandible with saw-toothed edge, anterior view, X250; 23, left mandible with rounded teeth, anterior view, X250; 24, phantom side view of anterior end of larva with full trophothylax, X28; 25, phantom side view of anterior end of larva with empty trophothylax, X28; 26, larva in side view, X28.



First-Instar Larva: Straight length about 0.9 mm. (Egg 1.13 mm. long and 0.225 mm. wide). Straight, largest at the anterior end, tapering gradually to the posterior end which is narrowly rounded; head anteroventral; trophothylax present. Head relatively very large; cranium sub-ovoid, genae slightly bulging. Head hairs less numerous (about 70) and shorter (about 0.009 mm. long). Labrum twice as broad as long and with a straighter ventral border. Mandible relatively shorter and with three sharp denticles, two apical and one lateral. Otherwise similar to the mature larva.

Second-Instar (?) Larva: Straight length about 1.3 mm. Head more ventral; food present in some trophothylaxes. Otherwise similar to the first instar larva.

Material studied: Numerous larvae from Ceylon, courtesy of Dr. W. L. Brown.

***Tetraponera allaborans* Walker**

Pl. III, figs. 17-21

Similar to *aikeni*, except in the following details: Apparently somewhat slipper-shaped in ventral view, widest at abdominal somite VI. Leg, wing and one pair of gonopod vestiges present. Body hairs (1) a little longer (0.03-0.052 mm.); (2) 0.15-0.2 mm. long, two to four on each somite except abdominal somites IX and X; (3) 0.096-0.15 mm. long, two to four on the mesothorax, metathorax and each abdominal somite I-VII, with numerous minute denticles on the distal $\frac{2}{3}$ of the shaft of some hairs. Head hairs more numerous (about 144). Labrum twice as broad as long, with a patch of spinules in short subtransverse rows on each ventrolateral surface. (Material studied: several damaged integuments from Los Baños, Philippine Islands.)

Wheeler and Bailey, 1920:—"Head rather rounded behind. Anterior maxillary sense-organs produced into slender, anteriorly directed points. Oncochaetae straight, without sigmoidal flexure, in four rows, a pair in each row, on each segment from the prothoracic to the sixth abdominal. Similar hairs, but without hooks, occur on the seventh to the ninth abdominal segments. Acrochaetae absent. Microchaetae short and sparse, much longer on the head and somewhat longer on the prothorax than on the more posterior segments" (p. 258). "Practically all of the pellets of this species consist of fragments of small insects, among which pieces of chitin, detached mandibles, and pieces of eyes and hairs can be recognized. Pollen, fungus spores and pieces of mycelium occur in very few instances" (p. 261). Fig. 4D (p. 257) head of larva in anterior view. Pl. fig. 29, photomicrograph of portion of larval pellet.

***Tetraponera clypeata* Emery**

Emery, 1899, described briefly (pp. 6-7) this larva; see above under the subfamily.

***Tetraponera natalensis* F. Smith**

Emery, 1899, described briefly (pp. 6-7) this larva, see above under the subfamily. Plate II, Fig. 7a-e, larva in side view, three views of portions of the head and an antenna. The figure of the larva in side view (7a) was used by Berlese, 1925, Vol. II, as Fig. 825A on p. 846; by Escherich, 1906, as Fig. 30E on p. 74 and 1917 as Fig. 36E on p. 96. Berlese, Emery and Escherich all use the old generic name *Sima*.

***Tetraponera rufonigra* (Jerdon)**

Dutt, 1912, p. 249:—"Larvae are white, cylindrical, with ends rounded, 5 mm. in length. There is a fine minute longitudinal black line above extending over a few segments of the body in the middle. The integument is transparent and through it is visible a black ring encircling the central portion of the body. The head is bent downwards and rests on the ventral side, forming an emargination in the convexity of the undersurface." This description is under the old generic name *Sima*.

***Tetraponera* sp.**

Pl. III, figs. 22-26

Similar to *aikeni* except as follows: Straight length about 3.7 mm. Not quite so slender. Mesothoracic and first abdominal spiracles the largest. Body hairs (1) minute (0.009-0.027 mm. long); (2) 0.018-0.21 mm. long, some on every somite; (3) two on prothorax, six on meso- and metathorax, six to eight on the first abdominal somite and six or seven on the second abdominal somite. Head hairs not quite so numerous (about 86). Antennae larger (but still small). Mandible quadrangular in anterior view; proximal half only slightly swollen, distal half straight, with only the teeth on the apical portion turned medially; apical tooth more prominent; medial edge serrate or all teeth blunt and rounded; anterior surface with prominent denticles. Maxillary palp represented by a low flat cluster of five sensilla. Labium small, with a few arcuate rows of minute spinules on the anterior surface; an isolated sensillum between each palp and the opening of the sericteries. (Material studied: numerous larvae from Port Sudan, Red Sea, 22-VI '39, N. A. Weber No. 1217.)

***Tetraponera* sp.**

Mature Worker Larva: Straight length about 4.3 mm. Similar to *aikeni* except as follows: Body hairs (1) 0.006-0.012 mm. long; (2) 0.009-0.31 mm. long, two to four on each thoracic and each abdominal somite I-VI, ten on somite VII, six on somite VIII. Integument with minute spinules in transverse rows on the ventral surface of the thorax and abdominal somite I. Cranium subcircular in anterior view. Head hairs nearly twice as numerous (about 180) and

shorter (0.006-0.018 mm.). Anterior surface of mandibles with a few denticles. Maxillary palp a tall cone with one apical, one subapical and three lateral sensilla. Anterior surface of labium with a few transverse rows of minute spinules.

Queen (?) Larva: Straight length about 4.6 mm. Similar to worker larva except as follows: Body slenderer; whole body often evenly curved ventrally; with a short transverse slit on the midventral surface of abdominal somite IX. Body hairs (1) as in worker larva; (2) and (3) mostly broken off. Integument of dorsal surface of abdominal somites I-III and of all surfaces of remainder of abdomen with short transverse rows of minute spinules. Head relatively smaller.

Male (?) Larva: Straight length about 4.4 mm. Similar to worker larva except as follows: Two pairs of gonopod vestiges present. Body hairs (2) ten on abdominal somites III-VI; eight on abdominal somites VII and VIII; four on IX. Whole integument sparsely spinulose, the spinules minute and in short transverse rows. Cranium subrectangular and slightly longer than wide.

Material studied: numerous larvae from Siabe River, Kenya, February 8, 1948, N. A. Weber No. 2053.

Genus *Viticola* Wheeler

Body long, slender and subcylindrical; head applied to the ventral surface near the anterior end; near the mouth parts is a swelling on each ventrolateral surface of each thoracic somite and abdominal somite I. Trophothylax well developed. Segmentation distinct. Integument of lining of trophothylax and dorsal surface of a few posterior somites spinulose. Body hairs numerous and uniformly distributed (except none on and adjacent to the trophothylax). Of three types: (1) simple, minute to short, the most numerous type; (2) simple, short to moderately long, 6-12 on each somite; (3) with sinuous shaft and one apical hook, 4-6 on each thoracic somite and on each abdominal somite I-VII. Cranium subhexagonal. Antennae small. Head hairs only moderately abundant, simple, short and not uniformly distributed. Labrum small, ventral border entire; anterior surface with two hairs and about ten sensilla, but apparently without spinules; ventral border with a few spinules and about six sensilla; posterior surface spinulose and with about ten sensilla. Mandible rather small; with one lateral and one apical tooth; the subapical medial border erose; a few minute spinules on the anterior surface. Maxilla small; apex directed medially, paraboloidal; with long slender spinules in short transverse rows; palp a slightly raised cluster of five sensilla. Labium short; each palp a slightly raised cluster of five sensilla.

Wheeler, 1922a, p. 108:—"Larva hypocephalic as in *Pachysima* and *Tetraponera* and like that of

the latter genus in the development of the exudatoria and dorsal hairs."

Viticola tessmanni (Stitz)

Text fig. 2, L-R

Worker (?) Larva: Long, slender, subcylindrical; head ventral, near the anterior end; near the mouth parts is a swelling on each ventrolateral surface of each thoracic somite and of the first abdominal somite. Trophothylax present; the first abdominal somite forms the sides of the pocket; the second abdominal somite extends anteriorly on the ventral surface of the flap of the pocket. Anus subterminal. Segmentation distinct. Mesothoracic spiracles the largest, the others slightly smaller and uniform in diameter. Body hairs rather numerous and fairly uniformly distributed. Of three types: (1) minute to short (0.009-0.108 mm.), simple, the most numerous type (few on the tenth abdominal somite), without alveolus and articular membrane; (2) simple, short to moderately long (0.036-0.117 mm.), six to twelve on each somite; (3) moderately long (0.12-0.234 mm.), sinuous, with a single hook, two or three on each dorsolateral surface of each thoracic somite and on each abdominal somite I-VII. Integument of posterior somites with minute spinules in short transverse rows, the spinules becoming shorter and the rows fewer anteriorly. Cranium subhexagonal in anterior view, widest above the level of the antennae. Head hairs only moderately abundant (about 38), simple, short (0.018-0.059 mm.), not uniformly distributed and lacking in a wide inverted Y. Antennae small, each a low convexity bearing three sensilla, each of which bears a minute spinule. Labrum rather small; twice as wide as long; each half of anterior surface with one short hair and four or five sensilla; each half of ventral border with three sensilla and a lateral patch of spinules in short subtransverse rows; each half of posterior surface with a loose cluster of five sensilla; posterior surface spinulose, the spinules in rows, the rows subtransverse dorsally, sublongitudinal ventrally, but with a small midventral naked area. Mandible small and rather stout; apical tooth short, rather blunt and curved medially; subapical tooth lateral, slenderer; subapical portion of medial border erose; anterior surface with a few spinules, some isolated and others in short rows. Maxilla rather small; apex paraboloidal, with rather numerous long very slender spinules in transverse rows; palp represented by a slightly raised cluster of five sensilla; galea represented by two sensilla on a slight elevation. Labium short; each palp represented by a slightly raised cluster of five sensilla; an isolated sensillum between each palp and the opening of the sericities; the latter a short transverse slit. Hypopharynx densely spinulose, the spinules slender

and in numerous subtransverse rows, the rows so close together that the spinules overlap.

Sexual (?) Larva: Similar to worker (?) larva, except as follows: Body plump, suboval, widest at abdominal somite IV or V, tapering gradually to the anterior end and more rapidly to the posterior end, which is narrowly rounded. Spiracles all small, the mesothoracic and first abdominal the largest and subequal, the others slightly smaller and subequal. Body hairs sparse, mostly minute. Of three types: (1) shorter (0.006–0.045 mm.); (2) longer (0.09–0.25 mm.); (3) 0.162–0.198 mm. Head hairs simple, sparse (about 28), mostly minute (0.006–0.027 mm.). Mandibles with the teeth and denticles less clearly defined.

Material studied: a dozen tattered integuments from the Congo.

Wheeler, 1918, p. 304:—"The adult larva differs little from the youngest. . . It is long, cylindrical and hypocephalic, i.e., with the head on the ventral side instead of being terminal. . . It has a pair of swollen appendages, belonging to the prothoracic segment and applied to the sides of the head, and a large protuberance, evidently representing a pair of fused appendages, on the ventral side of the first abdominal segment. The dorsal surface is furnished with long, hook-shaped hairs, by means of which the larva is evidently suspended from the walls of the nest." Fig. 6, on p. 304, a mature larva in side view. This figure was used by Carpenter, 1928 as fig. 62a on p. 244; by Wheeler 1922a as fig. 24, p. 112.

Wheeler, 1922a, pp. 111–112:—"The adult larva . . . resembles the larva of *Tetraponera natalensis* figured by Emery, but is longer and more slender and two of the postcephalic segments bear appendages, the significance of which is more fully explained in my remarks on *Pachysima*. The prothoracic segment bears a rounded appendage on each side and applied to the side of the head, which, as in the *Tetraponera* larvae, is over arched by the protuberant, cowl-like prothoracic segment. The first abdominal segment bears ventrally two large and very protuberant appendages which are fused with each other in the middle line. The anterior segments of the body have on their dorsal surfaces clusters of long hooked hairs, as in *T. natalensis*, and the more posterior segments have simple stiff hairs of very unequal length on their ventral surfaces. There are also numerous short, sparse hairs, scattered over the whole body. The young larvae are essentially like the oldest in form and pilosity. The mandibles are well chitinated and minutely bidentate at the tip as in *natalensis*, and the head bears minute rudiments of antennae on its dorsal surface. I find also that the larvae of certain East Indian *Tetraponerae*, e.g., *T. alloborans* (Walker), have a similar structure."

Wheeler and Bailey, 1920:—"Larva very

slender, with very prominent trophothylax and large rounded exudatoria on each side of it. Oncochaetae straight, four in number, in two pairs on each segment from the prothoracic to the sixth to eighth abdominal. Acrochaetae very long but unequal, numerous, on the side of each abdominal segment. Microchaetae short, unequal, scattered" (p. 258). "The insect substances in the pellets of these larvae resemble the yolk of ants' eggs and the fat-body of the larvae themselves, suggesting that some of the brood had been used as food for the more vigorous progeny. In one pellet pieces of the skin of a *Viticolia* larva could be clearly recognized. There are also spores and bits of hyphae in many cases and particles that seem to be pith and callous tissue. . . The absence from the *Viticolia* pellets of any clearly recognizable insect material obtained outside the myrmecodomatia may be very significant" (p. 261). Fig. 4E, on p. 257, head in anterior view. Fig. 6 (p. 268) shows a sagittal section through the anterior end of a larva, but Wheeler subsequently repeated it several times with the label *Pseudomyrma gracilis* (1922b as Fig. 62D, p. 401; 1923 as Fig. 62D, p. 170; 1926 as Fig. 30D, p. 239; 1928 as Fig. 43D, Pl. XXVII, facing p. 200). Brues, 1946, used the sagittal section as his fig. 25B on p. 198.

Genus *Pachysima* Emery

This genus, with only two species, cannot be satisfactorily defined. The characters which the mature larvae have in common (the trophothylax and the long slender body) are also present in all other Pseudomyrmecinae. The long slender shape is found in the larvae of many other genera inhabiting plant cavities and is, therefore, too general a character to be significant. The trophothylax, however, is distinctive for this subfamily. On the basis of mature larval characters *Pachysima latifrons* and *Pachysima aethiops* might well be in separate genera. However, the youngest larvae of both species have peculiar exudatoria (see Wheeler, 1922a, below).

Forel (1922, p. 83=1928, Vol. I, pp. 462–463) referred briefly to Wheeler's description of the exudatoria and to his discussions of trophallaxis in *Pachysima*.

Wheeler, 1922a, p. 113:—"Larva without hooked dorsal hairs; the exudatoria on the three thoracic segments and first abdominal segment in the youngest stage (trophidium) long and digitiform."

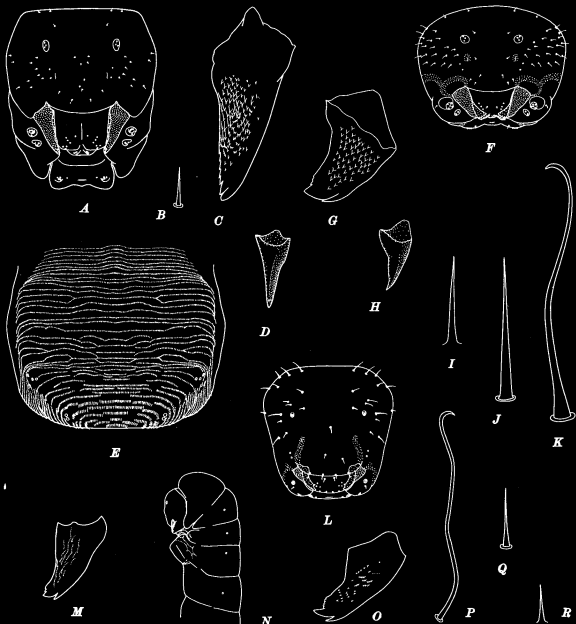
Pachysima aethiops (F. Smith)

Text fig. 2, A–E; 3 and 4

Estimated length 5.5 to 13.3 mm. Body apparently subcylindrical; head ventral, near the anterior end; near the mouth parts is a swelling on each ventrolateral surface of each thoracic somite and abdominal somite I; ventral surface of

abdominal somite II projecting anteriorly; the prothorax forming the anterior end and narrowly rounded; the posterior end tapering from about the eighth abdominal somite to the tenth, the latter forming the narrowly rounded posterior end. Anus subterminal. Gonopod vestiges present. Trophothylax apparently present. Seg-

mentation distinct. Spiracles small, the mesothoracic the largest, the others slightly smaller and subequal. Body hairs sparse and apparently all of one type: simple, minute (0.006-0.072 mm. long), with alveolus and articular membrane. Cranium suboctagonal in anterior view; nearly twice as broad as long, widest just below the



TEXT FIG. 2

Pachysima aethiops (F. Smith), FIGS. A-E.—A, head in anterior view, X39; B, body hair, X278; C, left mandible in anterior view, X143; D, left mandible in medial view, X72; E, labrum in posterior view, X163.

Pachysima latifrons Emery, FIGS. F-K.—F, head in anterior view, X39; G, left mandible in anterior view, X143; H, left mandible in medial view, X72; I-K, three

types of body hairs, X278.

Vilticicola tessmanni (Stitz), FIGS. L-R.—L, head in anterior view, X82; M, mandible of sexual (?) larva, in anterior view, X278; N, phantom view of anterior end of larva with empty trophothylax, X22; O, mandible of worker (?) larva, in anterior view, X278; P-R, three types of body hairs, X278.

antennal level. Head hairs only moderately abundant (about 50) and concentrated in small clusters (*i.e.*, not uniformly distributed), simple, slightly curved, very slender, minute (0.006–0.036 mm. long). Antennae rather small, slightly elevated, each with three sensilla, each bearing a minute spinule. Labrum quadrangular (breadth 1.25 times length); with a median ventral projection; lateral borders sinuate; each half of anterior surface with six sensilla; each half of ventral border with three or four sensilla; each half of posterior surface with about five sensilla; all surfaces spinulose, the spinules shorter and in shorter subtransverse rows on the anterior and lateral surfaces and on the ventral border; posterior surface with longer spinules in longer and more numerous rows, the rows transverse dorsally, longitudinal ventrolaterally. Mandible straight, subtriangular in anterior view; apex forming a short straight tooth; a subapical tooth and several denticles on the medial surface;



TEXT FIG. 3. *Pachysima aethiops* (F. Smith), A, first larval stage, in ventral view; B, first larval stage, in side view. (Wheeler, 1918, Fig. 7, p. 305.)

anterior surface with numerous spinules, the spinules isolated or in short subtransverse rows. Maxilla large; with a large projection directed downward and backward; apex small, rounded, directed medially, with numerous short encircling rows of spinules, the spinules longer on the posterior surface; palp a large knob (bearing four sensilla) mounted on a slight elevation (bearing one sensillum); galea represented by two sensilla on a slight elevation. Labium projecting, subrectangular; with short arcuate subtransverse rows of spinules on the anterior surface; palp represented by three or four sensilla on a slight elevation; a minute hair between each palp and the opening of the sericteries; the latter a short transverse slit on the anterior surface. Hypopharynx with numerous subtransverse rows of

many fine spinules. (Material studied: a dozen tattered integuments from the Congo.)

Emery, 1912, pp. 97–98:—"Ce sont des exemplaires arrivés au maximum de nutrition et prêts à se changer en nymphe; du moins, je le pense; je crois interpréter correctement un appendice plat, sous le segment pronotal, en disant que c'est l'ébauche des pattes antérieures. Cette larve est beaucoup moins hypocéphale que celle de *S. [Sima] Tetraponera natalensis*, que j'ai décrite et figurée dans mon mémoire de 1899; la larve de *S. aethiops*, du moins les individus que j'ai sous les yeux, a fort peu de poils et des poils très courts." Fig. 2, p. 97: larva in side view and anterior end of larva enlarged. Wheeler (1918, p. 308) discussed Emery's conclusions (see below).

Wheeler, 1918:—"The meaning of the thoracic and abdominal appendages becomes clear when we examine the larvae of *Pachysima aethiops* and *latifrons*. Four distinct stages, probably separated by moults, or ecdyses, may be recognized in *aethiops*. The first stage larva, just after hatching, is represented in Fig. 7 as it appears in ventral and lateral view. The body is curved, convex dorsally and concave ventrally, and terminates behind in a cylindrical projection, with the anus shifted to the ventral surface near its base. The creature is strongly hypocéphalic. The head is surrounded by a cluster of prominent, tubercle-like appendages. On the prothorax, which is large and forms a great hood over the head, there are three pairs of these appendages, an anterior truncate pair, a median pointed pair and a large posterior pair, swollen and rounded and embracing the sides of the head. These evidently correspond to the single prothoracic pair of the *Tetraponera* [= *Viticicola*] *tesmanni* larva. The mesothoracic segment has a pair of smaller appendages nearer the mid-ventral line. Between them arises a very peculiar organ with a swollen, pear-shaped base prolonged into a slender, apparently erectile, tentacle-like process which extends up in front of the head and terminates in a small ampulla. The first abdominal segment bears a pair of large swollen appendages lying at the base of the mesothoracic pair and united with a large and very prominent mid-ventral tubercle. This tubercle and its lateral appendages are represented in the *T. tesmanni* larva but the others, with the exception of the third prothoracic pair, are absent. Sections and stained, cleared preparations of the whole larva show that the various tubercles contain portions of the fatbody, at least in the bases of their cavities, and next to the hypodermis a dense, granular substance, evidently a coagulated liquid produced by the underlying adipocytes, or trophocytes. The same liquid also fills the unpaired tentacle, except its pear-shaped base, which contains fat cells. Around the bases of the tubercles are muscles so

arranged that their contraction must increase the pressure on the fat and granular liquid and in all probability cause the latter to exude through the hypodermis and delicate chitinous cuticle onto the surface. The whole arrangement of the tubercles, in fact, constitutes a system of exudate organs, or exudatoria,¹² as I shall call them, adapted to secrete substances that can be licked up by the ants when they are feeding and caring for the larvae. In this stage the mandibles are small, soft, blunt and unchitinated so that the larva must be fed with regurgitated liquid food. The labium has a peculiar pair of fleshy appendages, shown just beneath the mandibles in 7A. The body is naked, except for a few sparse, pointed bristles on the dorsal surface and the median pair of prothoracic appendages. As nothing like this larval stage is known among ants or indeed among the Hymenoptera, I propose to call it the 'trophidium.'

"The second stage larva is shown in Fig. 8A. The various exudatoria are smaller in proportion to the remainder of the body but are still much like those of the trophidium. The body is more elliptical, the mandibles are more pointed and distinctly falcate, but even in this stage they are unchitinated and therefore nonfunctional. The coarse hairs are visible on the dorsal surface but a more uniform investment of small hairs has made its appearance. They are blunt or even clavate, especially on the prothoracic segment. In this and the trophidium stage I am unable to find any salivary glands in cleared preparations though rudiments may, perhaps, be present.

"The third stage larva (Fig. 8B) is larger and very regularly elliptical. The exudatoria can all be recognized, except the unpaired tentacle. It is, however, present in some of the younger individuals but in a greatly reduced and vestigial condition and at the bottom of the depression which now appears as a definite pocket just back of the mouth and under the midventral swelling of the first abdominal segment. In many larvae I found in this pocket a small, rounded, dark-colored pellet, which puzzled me at first. In sections, however, it was at once seen to consist of the triturated and compacted bodies and parts of small insects. It is, in fact, a food-pellet placed by the worker ants in the pocket just behind the larva's mouth. In this stage, therefore, the larva is fed on solid food and the strongly chitinated, acute and bidentate mandibles corroborate this statement. Slender salivary glands may also be detected, indicating that the substance of the food-pellet is subjected to extraintestinal digestion. The longer hairs on the dorsal integument have almost completely disappeared. The first pair of appendages on

the prothorax has disappeared and the second pair is obsolescent.

"In the fourth, or adult stage (Fig. 8C) the larva is more elongate and cylindrical and much more hypocephalic, the prothorax forming a great protuberance in front of the head. The exudatoria are still recognizable, with the exception of the first and second prothoracic pairs, which have disappeared entirely. The labial appendages are reduced. A food pellet was found in the postcephalic pocket in several of the larvae of this stage but is not represented in the figure. The coarse hairs have disappeared from the integument, which is now uniformly covered with very short, delicate hairs, and the structure of the posterior end of the body is very different from that of the preceding stages.



TEXT FIG. 4. *Pachysima aethiops* (F. Smith). A, second larval stage, in ventral view; B, third larval stage, in ventral view; C, mature worker larva, in ventral view. (Wheeler, 1918, Fig. 8, p. 307.)

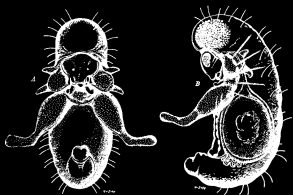
"We owe the only account of the *aethiops* larva in the literature to Emery (1912). He describes what corresponds to my fourth stage larva very briefly and figures its anterior end with some of the exudatoria, but erroneously interprets the large prothoracic pair as 'ébauches de pattes,' or rudiments of the anterior pair of imaginal legs" (pp. 305-308). This description was repeated in essentially the same form by Wheeler, 1922a, pp. 116-119; the figures were repeated as Fig. 26, p. 115 and Fig. 27, p. 117, but the letters designating the third and fourth stage larvae were interchanged. Eidmann (1944, p. 440) discussed briefly Wheeler's descriptions and conclusion. We are reproducing Wheeler's Figs. 7 (p. 305) and 8 (p. 307) as Text figs. 3 and 4.

Wheeler, 1928, p. 234:—"The exudatoria . . . are greatly developed in the very young larvae (trophidia) . . . but decrease rapidly in size in

¹²This is apparently the first place the exudatoria were named.

the later stages when the salivary glands develop and apparently usurp their secretory function." [= Wheeler, 1926, p. 282.]

Wheeler and Bailey, 1920:—"In large larvae there seem to be no traces of oncochaetae or acrochaetae. Microchaetae short, of unequal length. Head rather subrectangular, mandibles broader than in the other three genera and the sense-organs of the maxillae appearing as distinct though low tubercles. Labrum trapezoidal, its anterior border truncate, entire" (p. 258). "Practically every pellet examined contains pieces of Coccids or the crumpled-up bodies of entire young Coccids. Fungus spores and pieces of mycelium are often abundant as are also pieces of plant-tissue, evidently gnawed from the walls of the cavities (myrmecodomatia) inhabited by the ants. In a few of the pellets the junior author also found small Nematodes resembling the species of *Pelodera* described by Janet as



TEXT FIG. 5. *Pachysima latifrons* Emery, A, first larval stage, in ventral view; B, first larval stage in side view, (Wheeler, 1918, Fig. 9, p. 309.)

living both as parasites in the pharyngeal glands of certain European ants and as free organisms in the detritus of the nest" (pp. 261-262). Fig. 4B, head in anterior view. Pl. figs. 1, 3, 10, 13, 14, and 37, photomicrographs of portions of larval pellets.

Pachysima latifrons Emery

Text fig. 2, F-K; 5 and 6

Estimated length: 7.75 mm. Body probably subcylindrical; head ventral, near the anterior end; with a ventrolateral swelling on each side of each thoracic somite and of abdominal somite I, the last with a terminal digitiform projection; the ventral surface of abdominal somite II extends anteriorly between the swellings on abdominal somite I. Trophothylax present. One pair of gonopod vestiges present. Body hairs moderately numerous and uniformly distributed except on the ventral surface of the thorax and abdominal somite I. Of three types: (1) simple, minute to short (0.009-0.108 mm.), without alveolus and articular membrane, the most

numerous type; (2) simple, moderately long (about 0.153 mm.), a few on most somites; (3) with sinuous shaft and single apical hook, moderately long (0.156-0.25 mm.), four in a transverse row across the dorsal surface of the metathorax and six on each abdominal somite I-VI or I-VII. Integument of the dorsal surface of the posterior somites spinulose, the spinules minute and in short transverse rows. Cranium short and broad (breadth 1.6 times length), occipital border rounded; narrowed, ventrally. Head hairs short (0.018-0.09 mm.), moderately numerous (about 65), mostly below the level of the antennae. Antennae rather small, each a low drumlin bearing three sensilla, each of which bears a minute spinule. Labrum small, narrowed ventrally, trilobed; each half of anterior surface with three or four sensilla and a minute hair; ventral border spinulose, each half with three or four sensilla; each half of posterior surface with five or six sensilla; posterior surface densely spinulose, the spinules long and in subtransverse rows. Mandible small, slightly curved both medially and posteriorly; apex a short blunt tooth with one rounded tooth laterally and a few rounded denticles medially; anterior surface with moderately numerous isolated spinules in oblique rows giving an imbricated appearance. Maxilla with the apex conical, directed medially and covered with numerous exceedingly minute spinules; palp a knob bearing five sensilla; galea a slight elevation with two sensilla. Labium short and broad; palp a slight elevation bearing sensilla; a minute hair between each palp and the opening of the sericteries; the latter a short transverse slit. Hypopharynx densely spinulose, the spinules abundant and in numerous long subtransverse rows. (Material studied: five damaged integuments from the Congo.)

Wheeler, 1918:—"The larvae of *Pachysima latifrons* are quite as extraordinary as those of *aethiops* and also pass through four stages. The trophidium, or first stage, shown in Fig. 9, is very hypocephalic, the prothoracic segment being greatly enlarged and projecting anteriorly. Both preparations stained *in toto* and sections show that the portion of the fat-body in this segment is sometimes heavily charged with urate crystals, so that it undoubtedly functions as a storage kidney till the Malpighian vessels are sufficiently developed to excrete. The first and second pairs of prothoracic appendages of the *aethiops* larva are absent, but the third pair is very large and embraces the sides of the head. The meso- and metathoracic segments each bear a pair of slender pointed appendages, the first abdominal segment a huge leg-like pair, which are swollen and fusiform at the base and run out into a long slender process which forms an obtuse angle with the basal portion. The sternal region between these appendages is protuberant and its cuticular covering, like that of the four pairs

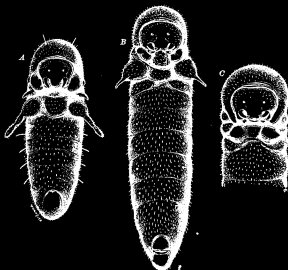
of appendages is minutely prickly, unlike the smooth cuticle of the remainder of the body. Sections show that both the appendages and the sternal swelling are exudate organs, though the prothoracic and abdominal pairs are much more important than the others. The prothoracic appendages are filled with blood and very little fat tissue, but their hypodermis is much thickened and consists of crowded cells arranged in peculiar clusters . . . The fusiform base is filled with large, clear trophocytes, or fat-cells, some of which in the middle of the swelling may contain urate crystals, like those in the prothoracic storage kidney, but the slender, tubular distal portion contains a granular liquid, which can only be regarded as an exudate derived from the trophocytes in the basal enlargement. This exudate is evidently filtered through the thin cuticula covering the appendage by pressure, for there is a rather elaborate system of muscles, as in the *aethiops* larva, surrounding the bases of the appendages and capable of subjecting their contents to pressure. The head is small and has soft, blunt, rudimentary and unchitinated mandibles, and the labium bears a pair of long, palp-like appendages, which project forward in the deep depression between the head and the swollen sternal portion of the first abdominal segment. These are probably also exudatoria and seem roughly to correspond to the unpaired tentacle of the *aethiops* larva. The structure of the mouth-parts shows that the larva in this stage is fed with liquid food regurgitated by the workers. The convex dorsal surface is beset with sparse, curved bristles of uniform thickness, with blunt tips. The segmentation of the body is indistinct and its posterior end curves forward and terminates in a large tubercle with the anal orifice just anterior to its base. Fig. 9B, drawn from a stained and cleared preparation, shows the nervous system and alimentary canal. The Malpighian vessels have only just begun to develop at the blind end of the proctenteron where it abuts on the posterior end of the large, elliptical mesenteron, or stomach, but no salivary glands can be detected.

"In the second stage larva (Fig. 11A) the body is more elongate and cylindrical and the four pairs of appendages can still be recognized though considerably smaller in proportion to the remainder of the body. The mandibles are becoming chitinated. Many of the long hairs on the dorsal surface are still present but a general covering of short, sparse hairs has made it appearance.

"The third stage larva (Fig. 11B) is larger and still more elongate and cylindrical and shows a further regressive development of the exudatoria. Those on the meso- and meta-thoracic segments have disappeared and the abdominal pair has short broad bases with the distal portions attenuated to slender points.

The labial appendages have also disappeared. The mandibles are well chitinated and the larva is now fed with pellets of crushed insects, like the *aethiops* larva in the corresponding stage. These pellets were found *in situ* in several of the alcoholic specimens as represented in Fig. 11B. The pellet lies in the deep pocket between the head and the sternal protuberance of the first abdominal segment and is therefore within easy reach of the mandibles and labium of the larva. Cleared preparations show that the salivary glands have made their appearance, though they are small and slender.

"The anterior end of the fourth stage, or adult larva is shown in Fig. 11C. The exudatoria of the prothoracic segment now appear merely as a pair of welts or folds embracing the sides of the head and continuous with the more dorsal portions of their segment, which is relatively smaller and less projecting than in the preceding



TEXT FIG. 6. *Pachysima latifrons* Emery. A, second larval stage, in ventral view; B, third larval stage, in ventral view; C, anterior end of mature larva, in ventral view. (Wheeler, 1918, Fig. 11, p. 311.)

stages. The exudatoria of the first abdominal segment are still distinct but their distal portions are reduced to mere points, sometimes absent in larvae just before pupation, and the sternal swelling is much less prominent. In this stage the larva resembles that of *Tetraponera* throughout its various stages. In the third and fourth stages of the *latifrons* larva, as in the corresponding stages of *aethiops*, the salivary glands probably furnish secretions which are useful both in the extraintestinal digestion of the food pellet and as substances that can be imbibed by the workers. The fact that in the two species of *Pachysima* the exudatoria decline *pari passu* with the development of the salivary glands certainly

suggests that both sets of organs have to some extent a common function" (pp. 308-312).

Fig. 9 (p. 309) and Fig. 11 (p. 311) are reproduced here as Text figs. 5 and 6. Fig. 10 (p. 310) shows a longitudinal section through an exudatorium of a first stage larva. The above description was repeated in essentially the same form by Wheeler, 1922a, pp. 121-124 and the figures appeared as Figs. 29-31. Bischoff (1927, p. 94) mentioned Wheeler's description and trophallaxis and adapted his Fig. 9 as Fig. 45, p. 95. Eidmann (1936, p. 36) referred to Wheeler's description and to trophallaxis. Imms' Fig. 13 (1931, p. 63) was adapted from Wheeler's Fig. 11B. Metcalf and Flint, Fig. 295 (1932, p. 447) repeated his Fig. 9. Wheeler repeated his Figs. 9 and 11 in 1922b as Fig. 63, p. 402 and Fig. 64, p. 403; in 1923 as Fig. 63, p. 171 and Fig. 64, p. 173; in 1926 as Fig. 39, p. 281 and Fig. 40, p. 282; in 1928 as Plates XXXV and XXXVI, between pages 234 and 235.

Wheeler, 1928, p. 234: "The exudatoria . . . are greatly developed in the very young larvae (trophidia) . . . but decrease rapidly in size in the later stages when the salivary glands develop and apparently usurp their secretory function." [= Wheeler, 1926, p. 282.]

Wheeler and Bailey, p. 1920: "In large larvae the oncochaetae are present, but very short, stout, curved or feebly sigmoidal, eight on each segment from the metathoracic to the seventh abdominal. Acrochaetae absent; microchaetae much longer than in *aethiops*. Head transversely elliptical. Mandibles broader and flatter, with broad, blunt apical tooth. Papillae bearing the maxillary sensillae less prominent. Labrum with more rounded anterior border" (p. 259). "This species is much rarer than the preceding but seems to have very similar habits. Of the two pellets examined, one contains fragments of Coccids, some spores, bits of mycelium, pollen grains and some pith tissue, with amber-colored cell contents; the other contains much the same substances together with a few Nematodes" (p. 262). Fig. 4C (p. 257), head of larva; Pl. fig. 16, photomicrograph of portion of larval pellet.

A BIBLIOGRAPHY OF THE LARVAE OF THE SUBFAMILY PSEUDOMYRMECINAE

- Berlese, A. 1925. Gli insetti. Vol. II. 1x+992 pp., 7 pls., 895 text figs. Milano: Società Editrice Libraria.
- Bischoff, H. 1927. Biologie der Hymenopteren. viii+598 pp., 244 figs. Berlin: Julius Springer.
- Brues, C. T. 1946. Insect dietary. xxi+446 pp., 22 pls., 68 text figs. Cambridge: Harvard University Press.
- Carpenter, G. H. 1928. The biology of insects. xv+473 pp., 16 pls., 88 text figs. London: Sidgwick & Jackson, Ltd.
- Creighton, W. S. 1950. The ants of North America. Bull. Mus. Comp. Zool. Harvard College 104: 1-585, 57 pls.
- Donisthorpe, H. 1921. The subfamilies of Formicidae. Proc. Entom. Soc. London, xl-xlvi.
- Dutt, G. R. 1912. Life histories of Indian insects. Mem. Dept. Agric. India, Entom. Ser. 4: 183-267, 4 pls., 22 text figs.
- Eidmann, H. 1936. Ökologisch-faunistische Studien an südbrasilianischen Ameisen. Arb. Phys. Anst. Entom. Berlin-Dahlem 3: 26-48, 81-114, 1 pl., 5 text figs.
1944. Die Ameisenfauna von Fernando Poo. Zool. Jahrb. Abt. Syst., Ökol. Geog. Tiere 76: 413-490, 1 pl., 17 text figs.
- Emery, C. 1899. Intorno alle larve di alcune formiche. Mem. R. Accad. Sci. Ist. Bologna 8: 3-10, 2 pls.
1912. Etudes sur les Myrmecines. Ann. Soc. Ent. Belg. 56: 94-105, 5 figs.
- 1921-22. Fam. Formicidae, Subfam. Myrmecinae. Genera Insectorum, Pass. 174: 397 pp., 7 pls.
- Escherich, K. 1906. Die Ameise. Schilderung ihrer Lebensweise. xx+232 pp., 68 figs. Braunschweig: Friedr. Vieweg & Sohn.
1917. Die Ameise. (2nd ed.) xvi+348 pp., 98 figs. Braunschweig: Friedr. Vieweg & Sohn.
- Forel, A. 1922. Le monde social des fourmis du globe comparé à celui de l'homme. Tome 3. vii+227 pp., 8 pls., 2 col. pls., 28 text figs. Genève: Librairie Kundig.
1928. The social world of the ants compared with that of man. Translated by C. K. Ogden. 2 vols. 551+445 pp., 24 pls., 138 text figs. London and New York: G. P. Putnam's Sons, Ltd.
- Imms, A. D. 1931. Social behavior in insects. ix+117 pp., 20 figs. New York: Dial Press.
- Metcalf, C. L., and W. P. Flint. 1932. Fundamentals of insect life. xi+581 pp., 315 figs. New York: McGraw-Hill Co., Inc.
- Safford, W. E. 1923. Ant acacias and acacia ants of Mexico and Central America. Smithsonian Report for 1921: 381-394, 15 pls., 7 text figs.
- Wheeler, G. C. 1938. Are ant larvae apodous? Psyche 45: 139-145, 2 pls.
- Wheeler, W. M. 1918. A study of some ant larvae, with a consideration of the origin and meaning of the social habit among insects. Proc. Amer. Phil. Soc. 57: 293-343, 12 figs.
1920. The subfamilies of Formicidae, and other taxonomic notes. Psyche 27: 46-55, 3 figs.
- 1922a. The ants collected by the American Museum Congo Expedition. Bull. Amer. Mus. Nat. Hist. 45: 39-269, 22 pls., 76 text figs., 41 maps.
- 1922b. Social life among the insects. IV. Ants, their development, castes, nesting and feeding habits. Sci. Month. 15: 385-404, 23 figs.
1923. Social life among the insects. vii+375 pp., 116 figs. New York: Harcourt, Brace & Co.
1926. Les sociétés d'insectes: leur origine—leur évolution. vii+468 pp., 61 figs. Paris: Gaston Doin & Cie.
1928. The social insects, their origin and evolution. xviii+378 pp., 79 figs. New York: Harcourt, Brace & Co.
- Wheeler, W. M., and I. W. Bailey. 1920. The feeding habits of pseudomyrmecine and other ants. Trans. Amer. Phil. Soc. (Art. 4): 235-279, 5 pls., 6 text figs.